Spring 5-1-2018

Regional Variation in Migratory Behavior and Reproductive Output of The Gulf Of Mexico Blue Crab Spawning Stock

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REGIONAL VARIATION IN MIGRATORY BEHAVIOR AND REPRODUCTIVE OUTPUT OF THE GULF OF MEXICO BLUE CRAB SPAWNING STOCK

by

Adam Kemberling

A Thesis
Submitted to the Graduate School,
the College of Science and Technology,
and the School of Ocean Science and Technology
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Master of Science

May 2018

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ABSTRACT

The overarching goal of this research was to better understand the structure and boundaries of the blue crab stock(s) in the Gulf of Mexico, focusing on large-scale movements of spawning female crabs. Because spawning location is a primary determinant of larval transport pathways, understanding spawning locations and offshore movements of female blue crabs can inform stock identification and potentially clarify the somewhat conflicting population genetic information available for blue crabs. A large-scale mark-recapture study was conducted through the partnership of state/federal management agencies, the commercial fishing industry, recreational fisherman, tourists, and numerous academic institutions to shed light on the timing and movements of mature female blue crabs in the Gulf of Mexico. The direction of travel, travel distances, and travel rates were estimated for each region in the study area using novel analytical techniques. Crabs regularly migrated beyond the borders of their home state, providing further evidence of mixing of the different state-managed stocks. The endpoint of the spawning migration in the offshore Gulf of Mexico, and the importance of the offshore spawning stock has come into question. Offshore female blue crabs collected during the SEAMAP groundfish survey were found to be actively spawning, with fecundity estimates in a similar range to the inshore population. Higher offshore abundances were observed off the coast of Texas and Louisiana across all study years from 2001-2016. Increasing temperature and dissolved oxygen were positively correlated with higher abundance, and offshore abundance was consistently higher in the summer sampling period than the fall.

ACKNOWLEDGMENTS

I would first like to thank my major professor Dr. Zachary Darnell. It has been a long journey spanning multiple universities and I wouldn't have accomplished all that I was able to without his support and guidance. He provided me with this opportunity to grow and develop as a scientist and supported me along the paths that the research took me. I'd also like to thank my committee members Dr. Wei Wu, and Dr. Frank Hernandez for their wealth of knowledge, as well as their encouragement and support through this process.

For funding this research project, I would like to thank the National Oceanic and Atmospheric Administration. For assisting with the colossal task of tagging across most of the Gulf of Mexico, I'd also like to thank the great people at Texas Parks and Wildlife, Louisiana Department of Wildlife and Fisheries, Mississippi Department of Marine Resources, Alabama Marine Resources Division, and the Florida Fish and Wildlife Conservation Commission. The commercial crabbing community of the Gulf of Mexico for their assistance with tagging, and their willingness to share their time and expertise for the benefit of their target species. In addition to the faculty and staff of each and all Universities involved in this project as well. Without their passionate participation and cooperation, a study of this scale could not have been successfully conducted.

I would also like to acknowledge my lab family, the Craboratory, we've been through a lot together and I love and respect each of you.

DEDICATION

This work is dedicated to my family. To my mother, Mary and my older brother, John. You have always been a source of love and support for me. This would never have been possible without that. Thank you.

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CHAPTER I - INTRODUCTION

Animal movements, especially large-scale migrations, present unique challenges for scientists and managers assessing or managing a species' abundance. The scale of migratory patterns should be an important consideration for managers, as a clearly defined stock should be to a large degree homogenous with no significant emigration from or immigration to other sources (Gulland, 1969). The concept of a maximum sustainable yield that has dominated fisheries management strategies for several decades rests on the assumption of a discrete manageable stock, with the vital rates (growth, reproduction, natural mortality, carrying capacity) of the species informing the amount of harvest fisherman can remove without compromising the fishery (Carvalho & Hauser, 1994). For maximum effectiveness, management and assessment must occur at a biologically relevant scale that matches the geographic scale of the managed/assessed stock (Begg et al. 1999, Al-Humaidhi et al. 2013). Understanding the magnitude, direction, and route of migrations is then critical for successful management of a migratory species, especially in the context of management actions with a temporal and/or spatial component (e.g. season/area closures, spawning sanctuaries, migratory corridors, etc.).

Blue crabs (*Callinectes sapidus* Rathbun) support one of the largest commercial fisheries in the United States and exhibit a complex life cycle characterized by multiple migrations (Millikin & Williams, 1984; NMFS, 2016). Blue crabs occupy both estuarine and oceanic habitats at different stages of their life cycle (Hines et al., 1987; Moksnes & Heck, 2006). Inseminated female blue crabs undertake a seaward spawning migration to high salinity (>20) waters, where zoeae larvae hatch from eggs and are released by the

female (Millikin & Williams, 1984). Zoeae are transported offshore where they develop in the plankton for 30–50 days before undergoing metamorphosis to the megalopal stage (Costlow & Bookhout 1959). Megalopae ingress into estuaries and settle in seagrass beds, marsh edges, and other structured habitats, where they metamorphose to juveniles (Moksnes & Heck, 2006). The juvenile stages are characterized by continued up-estuary migration and dispersal (Pardieck et al., 1999). Adults primarily occupy these inshore habitats but may range into nearshore oceanic habitats (Millikin & Williams, 1984). Mating in blue crabs occurs in the lower salinity inshore habitats following the females terminal molt to maturity (Van Engel, 1958). Following this pubertal, molt females begin their seaward migration, utilizing selective tidal-stream transport to reach high-salinity areas of the lower estuaries and coastal ocean, where conditions are suitable for spawning (Tankersley et al., 1998). In higher latitudes, females may overwinter in the lower estuaries, finishing their seaward migrations the following spring once water temperatures have warmed sufficiently (Millikin & Williams, 1984; Aguilar et al., 2008).

Blue crabs support valuable commercial fisheries throughout much of their range. The blue crab fishery in the United States is consistently one of the top 10 most valuable commercial fisheries in the United States (NMFS 2016). Due to the economic importance of this fishery, and declining landings in many areas, much attention has been paid to the timing and location of the blue crab seaward migration as much of the spawning stock biomass of the species is spatially and temporally aggregated in a way that makes them particularly vulnerable to fishing pressures (Aguilar et al., 2005; Aguilar et al., 2008; Carr et al., 2004; Lipscius et al., 2003). For example, in Chesapeake Bay, females aggregate and overwinter in the lower bay, where they were targeted for many years in

the winter dredge fishery (Jensen & Miller, 2005). To protect the spawning stock, and maximize the opportunities for juvenile recruitment, management agencies have sought to identify the timing and habitat use of actively migrating and staging mature female blue crabs (Aguilar et al., 2005; Carr et al., 2004; Jensen & Miller, 2005). This work has led to the delineation of formal spawning sanctuaries and seasonal harvest restrictions like the closure of the winter dredge fishery in the Chesapeake Bay (Commonwealth of Virginia Marine Resources Division, 2008).

In the Gulf of Mexico, the estuaries are structurally and hydrodynamically distinct from their Atlantic Coast counterparts. Research on the environmental patterns behind female blue crab seaward migration and the larval dispersal patterns on the Atlantic coast have not been shown to be consistent with conditions in the Gulf of Mexico. In the strongly tidal estuaries of the Atlantic Coast, the blue crab spawning migration is driven by ebb-tide transport, where the crabs rely on tidal currents to decrease the energetic cost of migration and increase movement rate (Forward et al. 2003). Yet tides in the Gulf of Mexico are typically weak (0.03–0.5 m), with a large wind-driven component relative to the more predictable astronomical tides (Flick et al., 2003). Salinity is thought of as a primary driving factor for seaward migration, as larval survival drops steeply at salinities below 20 ppt. Salinity is quite variable across the Gulf of Mexico, due to gradients in freshwater inflow. The bay systems of South Texas, characterized by minimal freshwater supply, routinely have inverse salinity gradients as periods of low rainfall and high temperatures lead to high salinity waters deep within the estuaries. In contrast, the estuaries of Louisiana have much lower salinity, and full-strength seawater (35 ppt) may not be found until 10–20 kilometers offshore). The historic meanderings of the

Mississippi River in Louisiana created a dynamic coastline in which estuary systems drain seaward in every direction but north. The regional variation in coastline geography across the Gulf of Mexico has impacts on the mixing patterns of the nearshore waters, making it unclear what conditions are favorable for larval ingress, and how that varies on a regional scale. On the Atlantic coast the patterns are much cleaner and consistent with their North-South coast, and larval ingress can be associated with specific weather patterns (Epifanio, 1995). Water temperatures in the Gulf of Mexico are favorable for successful spawning more months of the year, and they remain warm enough for the fishery to remain open nearly year-round.

Blue crab fisheries in the Gulf of Mexico are managed at the state level, with each state monitoring, assessing, and managing its inshore populations independently. Tagging studies conducted on both the Atlantic and Gulf coasts identified that female blue routinely travel large distances as part of their spawning migrations (Aguilar et al., 2005; Steele, 1991), and fishery-independent surveys have sampled actively spawning females over 150 km from the coast (GSMFC; ASMFC; Ogburn & Habegger, 2015). Salinities can be quite low in the northern Gulf of Mexico, due to high freshwater inflows, which may drive migrating crabs farther from shore (Lake Pontchartrain Bay Foundation). The extent of this spawning migration into offshore waters is an important contributor to connectivity patterns. Zoeae are transported passively on currents. Thus, spawning locations, in the context of local wind and current patterns, are likely a primary determinant of recruitment locations. Additionally, offshore spawning likely leads to a greater level of mixing than would be expected if all females spawned within their home

estuaries and may indicate that the current spatial scale of management and assessment is not biologically appropriate for Gulf of Mexico blue crabs.

The Gulf States Marine Fisheries Commission (GSMFC) recently proposed a two- stock structure for the Gulf of Mexico, with the break between the stocks at Cape San Blas, Florida. This decision was driven primarily by a single mark-recapture study of adult females tagged along the Gulf Coast of peninsular Florida, which found that crabs migrated northwestward after emigrating from estuaries, but did not cross Cape San Blas. Although this two-stock structure was incorporated into the most recent Gulf-wide stock assessment (GSMFC 2013) and Fishery Management Plan (GSMFC 2015), it has not yet been validated, and represents a major data gap that hinders blue crab management efforts. Recognizing this, the GSMFC, the GSMFC Blue Crab Technical Committee (GSMFC-TC), and the Louisiana Department of Wildlife and Fisheries (LDWF) have identified studies of large scale migratory movements, connectivity, and stock structure as research priorities (GSMFC 2013, Bourgeois et al. 2014, GSMFC 2015). This research was designed to fill this knowledge gap.

The overarching goal of this research was to better understand the structure and boundaries of the blue crab stock(s) in the Gulf of Mexico, focusing on large-scale movements of spawning female crabs. Because spawning location is a primary determinant of larval transport pathways, understanding spawning locations and offshore movements of female blue crabs can inform stock identification and potentially clarify the somewhat conflicting population genetic information available for blue crabs.

Each chapter of this thesis is written in the form of an independent manuscript. As a result, some introductory material is repeated in multiple chapters. Chapter topics are as follows:

Chapter 2. Regional variation in migratory behavior of mature female blue crabs in the Gulf of Mexico.

Chapter 3. Distribution, abundance, and reproductive contribution of spawning female blue crabs in offshore waters of the Gulf of Mexico.

CHAPTER II - REGIONAL VARIATION IN MIGRATORY BEHAVIOR OF MATURE FEMALE BLUE CRABS

INTRODUCTION

Many marine and estuarine species undergo distinct migrations during some stage of their life history (Polovina et al., 2004). For commercially harvested migratory species, understanding the timing, extent, and route of migration is critical for successful fisheries management (Ustaoglu & Okumus, 2004). Management decisions related to temporal and spatial harvest restrictions or closures of a fishery rely critically on an accurate understanding of a species' migration patterns (Hartog et al., 2011). Additionally, both management and stock assessment efforts are most effective if conducted at the appropriate spatial scale, i.e., that matching the spatial scale of the stock, which is influenced heavily by migration patterns of the species (Medici et al., 2006; Stephenson, 1999).

One such migratory species, the blue crab, *Callinectes sapidus* Rathbun, supports the sixth largest commercial fishery in the United States, with over 160 million pounds harvested in 2016 for a dockside value of $218.9 million (NMFS, 2016). Blue crabs are managed on a state-by-state basis apart from the Chesapeake Bay region (which is managed jointly by Maryland, Virginia, and the Potomac River Fisheries Commission). Each state or regional management authority determines management goals and harvest restrictions for a stock assumed to be independent of other stocks. With increases in fishing pressure and a degradation of estuarine ecosystems over time (Bricker, Rice, & Bricker, 2014; Day et al., 2007; West, Blanchet, Marx, & Powers, 2016), some state and

regional populations have declined (GSMFC, 2013; Lipcius & Stockhausen, 2002). Difficulties in assessing stock structure and boundaries have arisen due to a lack of information on large-scale movements of adult crabs and larval dispersal patterns, as well as conflicting population genetic information (GSMFC 2013).

Blue crabs exhibit a migratory life cycle characterized by an inshore migration during the early juvenile stages and a seaward spawning migration by inseminated females (Millikin & Williams, 1984). Female blue crabs undergo a terminal molt to maturity and mating typically occurs immediately following this molt, although an unmated female can remain sexually receptive for 7–10 days (Van Engel, 1958). The female stores the sperm which will be used to fertilize all eggs produced in her lifetime. Female blue crabs are highly fecund, capable of producing up to 7 clutches of 700,000 to 6 million eggs (Prager et al. 1990; Darnell et al. 2009; Graham et al. 2012). Following mating and several weeks of foraging, females begin migrating towards higher salinity waters at the mouths of estuaries or in the surrounding nearshore waters. During this time, females use ebb-tide transport as an efficient means to travel seaward (Forward et al., 2005; Forward et al., 2003; Hench et al., 2004). Ebb-tide transport (ETT) is a form of selective tidal-stream transport, characterized by repeated ascents into the water column during ebb tide and remaining on the bottom during flood tide, that results in stepwise movement seaward with each successive ebb tide (Tankersley et al., 1998; Forward et al., 2003). ETT in migrating female blue crabs is driven by a combination of an endogenous circatidal rhythm and responses to environmental tidal cues (Hench et al. 2004, Darnell et al. 2012). In the strongly tidal estuaries of the Atlantic coast, female blue crabs are able to migrate using ETT at rates averaging ~5.4 km d^{-1} (Carr et al. 2004). During flood tides,

females walk directly opposed to incoming flood tides at rates around of ~0.25 m s-1 (Carr et al. 2004). Female blue crabs can spawn multiple times during their migrations (Hench et al., 2004; Darnell et al., 2009), and continue to migrate throughout the reproductive phase of their life cycle.

During a spawning event, millions of eggs hatch simultaneously, releasing larvae (zoeae) into the water column. Blue crab hatching success and larval survival is largely determined by salinity, dropping steeply below 20 ppt (Costlow and Bookhout 1959). Zoeae remain in surface waters and are dispersed by currents during their ~30–50 day developmental period (Williams et al. 1990; Pile et al. 1996). Following the zoeal stages, the larvae metamorphose into megalopae, which re-invade the estuaries utilizing selective tidal-stream transport (Millikin & Williams, 1984; Biermann et al. 2016). Blue crab larval dispersal is largely determined by the local wind and current movements during the zoeal stages (Epifanio, 1995). For this reason, the location of each spawning event is a large determinant of where juvenile blue crabs will eventually recruit, and thus contributes heavily to determining large-scale connectivity patterns among estuaries (Etherington & Eggleston, 2000).

The female blue crab spawning migration has been the subject of much study in the past 20 years, although most studies have focused on migratory mechanisms and patterns within estuaries. Less well understood are their movements once they exit the estuaries and move into the coastal ocean. After reaching offshore waters, females typically do not re-enter estuaries, but remain in coastal or offshore waters (Hench et al. 2004). Previous tagging studies and fishery independent surveys have been shown that mature females are both capable of, and commonly found, traveling large distances from

native estuaries (Aguilar et al., 2005; Ogburn & Habegger, 2015; Steele, 1991). In the Gulf of Mexico, mature female blue crabs are found as far as 150 km from shore in fishery independent trawl surveys (GSMFC, unpublished data). Previous mark-recapture studies have identified cases of females traveling from the Chesapeake Bay to as far south as Florida (Aguilar et al., 2005), where in contrast females on Florida's Gulf coast followed a distinct northwestward migration once out of the estuaries (Steele, 1991). Additional research in the Gulf of Mexico has shown high densities of female blue crabs off the coast of Louisiana on the Ship, Tiger, and Trinity Shoal Complex, thought to be important foraging grounds (Gelpi, 2009), but the significance of these offshore habitats and details surrounding these movements remain unclear. The current lack of information regarding movements once out of the home estuary, and the scale of movement once offshore, hinders larval transport models and accurate stock assessments.

Successful management of a harvestable fishing stock, like the state-managed blue crab fisheries of the Gulf of Mexico, rests on assumptions that the stocks are independent of one another with respect to mortality and recruitment (Begga, Friedland, & Pearce, 1999). The migratory behaviors of females could thus confound management efforts built on these assumptions, if their spawning migrations and the subsequent larval recruitment is shown to violate these assumptions. The purpose of this study was to examine regional movement patterns of female blue crabs between estuaries and offshore waters of the Gulf of Mexico. A mark-recapture study was conducted over two years and spanning all five Gulf states. The temporal and geographic information on the post-copulatory movements of female blue crabs sheds light on the timing and motivations for regional migratory patterns.

METHODS

To better understand migratory movements within and between estuaries and offshore waters, a Gulf-wide mark-recapture study was conducted over two years (2016–2017). Mature female blue crabs were tagged in each of the five U.S. states bordering the Gulf of Mexico, from as far south as Lower Laguna Madre, TX and as far east as Cedar Key, FL. Crabs were not tagged farther south along the Florida peninsula as this area was the subject of a previous mark-recapture study (Steele, 1991).

A total of 12,655 mature female blue crabs were tagged and released between February 2016 and December 2017. Crabs were tagged in collaboration with commercial fishermen and in existing fishery-independent survey programs as they migrated out of the estuaries towards higher salinity waters of the Gulf of Mexico (GOM). Tagging coverage was unequal at both temporal and spatial scales, with large clustered releases occurring due to the reliance on the assistance of commercial fisherman in efforts to maximize coverage. The largest effort was focused on the southeastern Louisiana and the Mississippi Sound/Pontchartrain Basin interface due to proximity to tagging headquarters, the willingness of fishermen in those areas to assist in research efforts, and the large number of blue crabs present in Louisiana compared to other areas. Of the 12,655 tags released 17.6% were tagged by individuals or state/federal agencies without the assistance of commercial fisherman, leaving a remaining 82.4% that were tagged to some degree in a space of known fishing pressure.

Crabs were tagged immediately upon capture and released within 1 km of the collection site. Tags were printed with contact information, a unique identification number, a request for recapture data, and an offer of a $5 reward. Each tag was attached

externally using stainless-steel wire wrapped around the large lateral spines (Figure 1). At the time of tagging, the following data were recorded for each crab: tag ID (a six-digit alphanumeric code), carapace width (measured between the tips of the lateral spines), latitude/longitude where released, molt stage (Table 1), and reproductive stage (Table 2), and any notes on an individual's health.

Figure 1. External Tags Used in Study.

Table 1

Molt Stage Index

Molt Stage	Description
0	Carapace easily depresses at the base of the lateral spines, carapace is clean and a bright egg-shell white color on abdomen.
1	Carapace fully hardened, no longer depresses under considerable pressure at base of lateral spine. Coloration white and free of most external fouling.
2	Carapace fully hardened. Slight staining and discoloration of abdomen and appendages.
3	Carapace considerably fouled, coloration a dark yellow to brown, no calcified fouling organisms
4	Heavily fouled with dark brown discoloration, calcified fouling organisms present.

Table 2

Reproductive Stage Index

Reproductive Stage	Description
0	No egg mass present. Ovaries not clearly visible with external inspection.
1	No egg mass present. Mature ovaries externally visible through carapace.
2	Egg mass present, coloration of egg mass bright orange or yellow.
3	Egg mass present, coloration of egg mass dull brown.
4	Egg mass present, coloration of egg mass dark-brown to black.

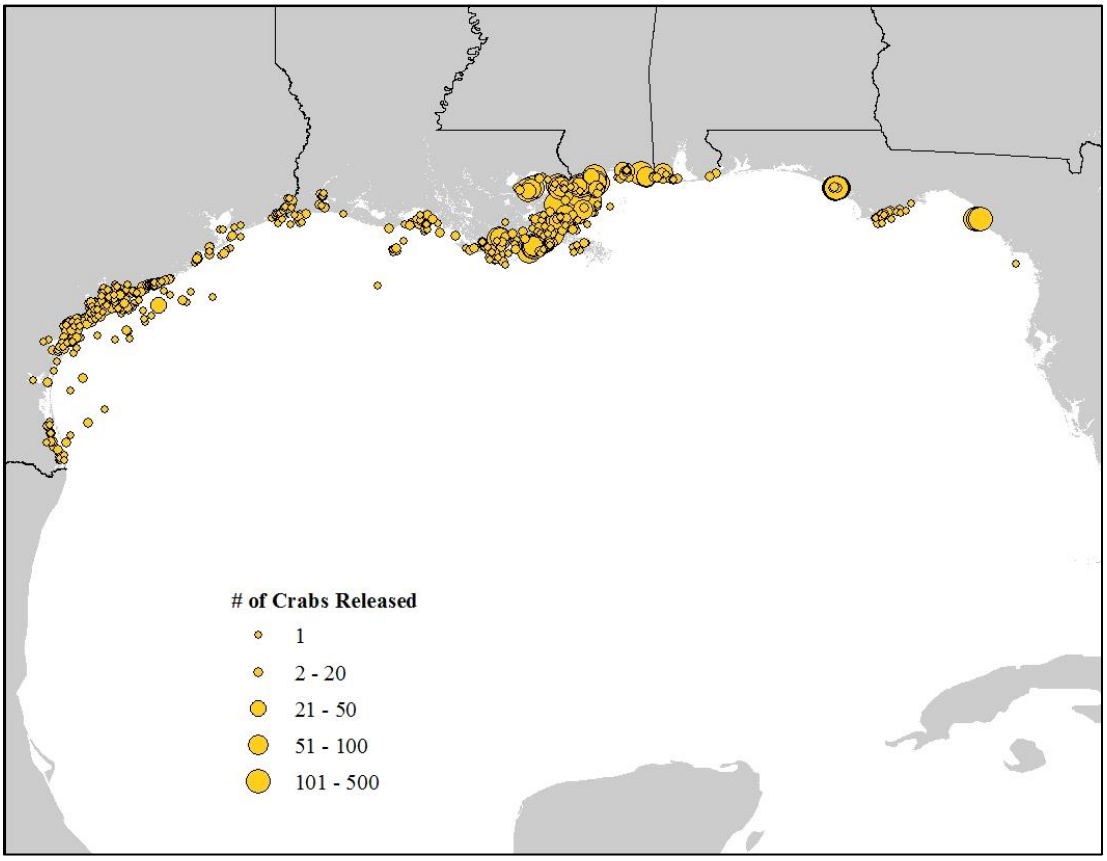

Figure 2. Tagging Study Coverage

Locations of tagging effort over full study period. Tagging effort was aggregated by day to emphasize the release of large numbers of tagged females.

Recaptures were obtained from commercial and recreational fishermen, state agencies, and the general public. The following data were requested for each recapture: date recaptured, location where recaptured, presence/absence of an egg mass, and egg mass color (if present), which can be used as a proxy for the developmental stage of the embryos. Because many crabbers do not have GPS units, recapture locations were often reported as a descriptive location. For recaptures reported with a descriptive location, an approximately latitude/longitude was assigned based on the reporting individual's

description. If only the name of a water body was given (typically a small bay), the approximate center of that water body was used as the recapture location. These locations were verified by mailing reporting individuals a map (or maps) so they were able to verify and/or correct our assigned location.

To assess the directionality of movement, the mean directions travelled were determined using the bearing between the initial tagging location and final recapture report. Crabs recaptured within 1 km of the tagging location were excluded from these analyses, as the resolution of our recapture data did not permit accurate analyses of movement at such a small scale. Direction and displacement data were then subset into two groups: crabs that were recaptured >1 but <15 km from the tagging site, and crabs that were recaptured >15 km from the tagging site. Rao's spacing tests were performed on each region subset to test whether the travel directions of recaptured females differed from a uniform circular distribution. Rayleigh z tests were then conducted on each of these two groups of crabs for each state and each basin with sufficient tagging and recapture numbers to assess whether migratory movements exhibited a distinct mean travel direction. The Rayleigh z statistic is calculated as $z = nr^2$, where n is the sample size and r is the mean vector derived from the following equations.

$$Y = \frac{\Sigma_{i=1}^{n} \sin_a}{n} \qquad X = \frac{\Sigma_{i=1}^{n} \cos_a}{n}$$

$$r = \sqrt{X^2 + Y^2}$$

X and Y are the rectangular coordinates of the mean angle, and r is the mean vector. The mean vector (r) is a measure of angular dispersion with values of zero corresponding to uniform circular dispersion and a value of one being a complete concentration in one

direction. The Rayleigh z statistic is used to test whether there is no sample mean direction (H_o) . Mean travel directions (θ_r) were then calculated for each of the subsets with sufficient data using the following equations.

$$\cos\bar{a} = \frac{X}{r} \qquad \sin\bar{a} = \frac{Y}{r}$$

$$\theta_r = \arctan\left(\frac{\sin\bar{a}}{\cos\bar{a}}\right)$$

Net migration rates were estimated using the distance traveled and the time between tagging and recapture (i.e., time at liberty). While previous studies typically estimate distance traveled as a straight-line distance between the tagging location and recapture location (Aguilar et at., 2005; Lambert et al., 2006), this method can greatly underestimate true travel distances. To more accurately measure distances traveled by migrating female crabs, the shortest possible over-water distance between the tagging location and the recapture location were estimated using least-cost paths (Darnell and Kemberling, *In Press*). NOAA C-Cap Land Cover Type raster layers were used to define the study areas as land or water cover at a 30 m x 30 m resolution to be used as the foundation for the cost raster. The cost-raster for the study area was weighted such that land cells had a prohibitively high travel cost (250) compared to all water cells (1). This cost-raster was then used to create a symmetric transition matrix for the study area, with 16-cell neighborhood movement allowed to increase the accuracy of the estimations. The transition layer and all least-cost distances were calculated using the "gdistance" package (Van Etten, 2015) in the R statistical environment (R Core Team 2016). If a recapture

was within a distance smaller than the resolution of the transition matrix, least-cost distances were set as equal to the Euclidean straight-line distances. Travel distances thus represent minimum possible over-water (i.e., not crossing land) distances between the tagging location and the recapture location. Net migratory rates were then calculated as the least-cost distance traveled divided by time at liberty for a conservative estimate of travel distance per day.

Based on the natural breaks in the tagging coverage, and the geography/hydrography of the study area, the mark-recapture data was divided into six regions. These regions were selected due to the natural clustering of tagging coverage, with the consideration of hydrographic boundaries like the Mississippi or Apalachicola Rivers. Texas was excluded from these analyses due to its small sample size (10 recaptured crabs) for such a large region.

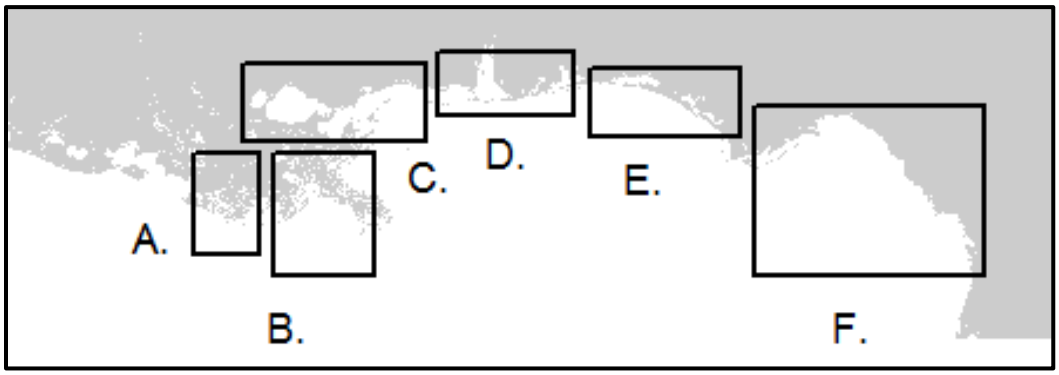

Figure 3. Mark-Recapture Study Regions

Study regions used for migratory analyses. Barataria basin (A), Terrebonne basin (B), Lake Pontchartrain & Eastern Mississippi Sound (C), Mobile Bay area (D), Florida panhandle (E), Big Bend Florida (F).

Sample sizes available for travel rate comparison ranged from 85 to 620 for the different tagging regions. Preliminary analyses showed that the distribution of travel rates

for all regions was skewed-right and non-normal. Bayesian methods were chosen for analysis because of the flexibility to compare variance among groups of different distributions and different sample sizes, and the ability to incorporate hierarchical structure while accounting for variance at each treatment level. By using a bayesian framework we can estimate how our variables of interest (travel rates) vary for each treatment level given all the available data collected. The end product is a probability distribution from which you can assess measures of central tendency (mean, median, 95% credibility intervals). While significance testing in Bayesian models is possible using credibility intervals, we believe the posterior probability distributions to be a more useful tool for visualizing how travel rates compared between regions and season. Both time at liberty and net movement rate were analyzed in a bayesian framework using the JAGS package (Hornik et al., 2003) in the R statistical environment (R Core Team 2016). JAGS (Just Another Gibbs Sampler) is used for Gibbs sampling of monte carlo chains. These chains iteratively explore parameter space using user-provided likelihood statements. To navigate towards more probabilistic values. At each iteration the sampler draws random values for the variable of interest for each chain in the model. By using the user-provided likelihood, the sampler determines whether the new value is more or less likely than the previous iteration. If the newly sampled value is more likely than the previous sample iteration, then the sampler will retain the new values. The random values are drawn from user provided distributions, which are typically informed by the sample data. In our case, travel rates were drawn from a gamma distribution because this mirrored the sample data collected, and because travel rates are a continuous and strictly non-negative variable. After several thousand iterations of the Gibbs sampling algorithm, each chain will have

navigated its way to the most likely values, and approximate posterior probability distributions can be compared. Diffuse gamma priors were set for all parameters in the JAGS model. Travel rate estimates and 95% credibility intervals were modelled as gamma distributed as a function of tagging region and tagging season. Tagging months of December–February were coded as the winter season, with March–May, June–August, and September–November corresponding to spring, summer, and fall tagging seasons respectively. Seasonal groupings were set to reflect temperature variation throughout the year, with the coldest three months set as the winter season, and the warmest three as the summer.

By using a hierarchical bayesian structure, travel rate estimates and confidence intervals reflect the intra-class variation of both regional and seasonal effects. All recapture travel rate measurements are used to inform a global (Gulf-wide) travel rate distribution. This global distribution can then be decomposed into season specific distributions, and further separated into region and season specific posterior distributions. Another advantage of the hierarchical structure is that areas with low tagging coverage for a season can still have travel rates estimated with probability-based credibility intervals. Because regional travel rates contribute to the larger seasonal grouping, areas with little or no data can be expected to show similar variability as the larger group distribution.

Although environmental variables were measured when tagging occurred, because crab traps are generally fished for a period of one or two days there was no way to verify that these measurements were consistent with the conditions present at the time the crabs entered the traps or how much they fluctuated between that that time and when

the traps were checked. Preliminary data analyses showed no correlation between our temperature, salinity, or dissolved oxygen measurements, and for these reasons they were not included as predictive covariates for travel rate.

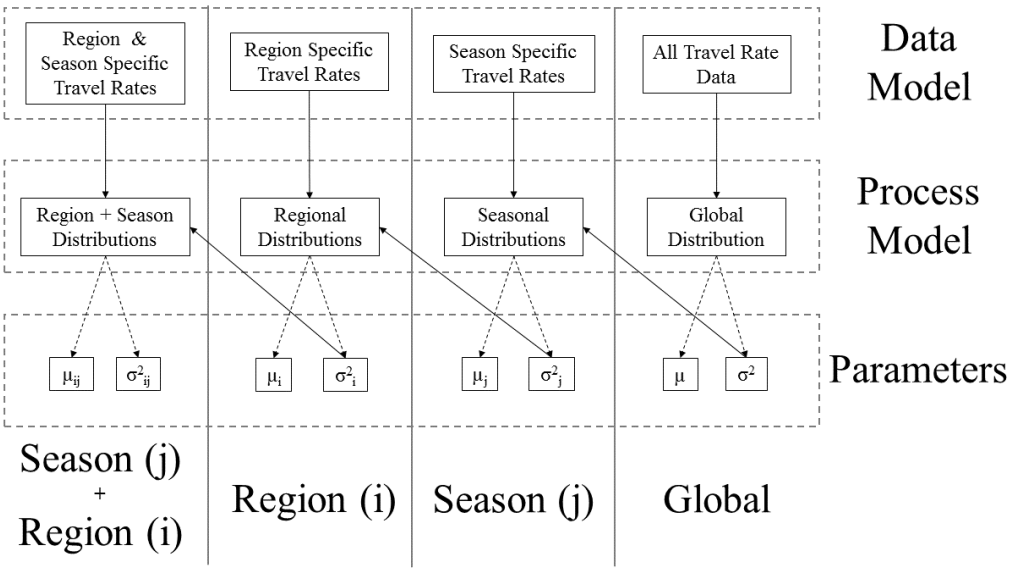

Figure 4. Travel Rate Directed Acyclic Graph

Directed acyclic graph of the multi-level model structure used to estimate travel rates by season and region. The gulf-wide distribution of travel rates is informed by all the data in the study. Travel rates at the gulf-wide level are distributed with mean (μ) and variance (σ^2). Each season is then given a vague prior with the global variance estimate to get the mean (μ_j) and variance (σ^2_j) for each season. Each seasonal distribution, in the absence of any new data will reflect the overall gulf distribution, and any data supplied for that season will inform the distribution to make it more season specific. Each regional and seasonal pairing has its mean (μ_{ij}) and variance (σ^2_{ij}) estimated using the mean estimate for each region (μ_i) with the seasonal variance estimate (σ^2_j) as its prior. By nesting the variance structures this way a Crab from region x and season y will have a travel rate estimate that is determined with respect to the distributions and variances of region x and season y.

RESULTS

Recaptures

A total of 1673 recaptures were reported with complete information, after exclusion of recaptures for tag numbers not found in our records or with un-usable location or time of recapture information, for a Gulf-wide recapture rate of 13.2%. Recaptures were reported by recreational fisherman, commercial fisherman including shrimpers and rod and reel fishermen, snorkelers, and beach combers (Table 3). Despite participation from a diverse group of stakeholders, the overwhelming proportion of recaptures were reported by commercial crabbers.

Table 3

Major reporter groups.

Report Type	**Number reported**	**% of Total**
Commercial crabber	1437	87.3
Commercial shrimper	42	2.6
Recreational (any)	124	7.5
State agency affiliate	27	1.6
Other	17	1

Recapture rates for each state ranged from between 13–24%, excluding Texas, which had an anomolously low 1% recapture rate. Tagging in Texas was entirely conducted by state/federal agencies during existing fishery independent surveys, rather than on commercial crab boats. This resulted in smaller numbers of crabs being released

at any given location, but a greater number of release locations. This may account for the anomolously low recapture rate observed in Texas. To assess this hypothesis, three recapture rates (# recaptured/# tagged) were calculated: (1) for crabs tagged in Texas through fishery-independent surveys, 10 recaptured/942 tagged = 1% recapture rate; (2) for crabs tagged in Louisiana through fishery-independent surveys, 17 recaptured/347 tagged = 4.9% recapture rate and (3) for crabs tagged in Louisiana through fishery-dependent methods, 752 recaptured/5536 tagged = 13.6% recapture rate. Louisiana was used for comparison because of large numbers of crabs tagged using both fishery-independent and fishery-dependent methods. Thus, recapture rates for Texas and Louisiana considering only crabs tagged in fishery-independent surveys are similar, and substantially lower than crabs tagged in Louisiana using fishery-dependent methods.

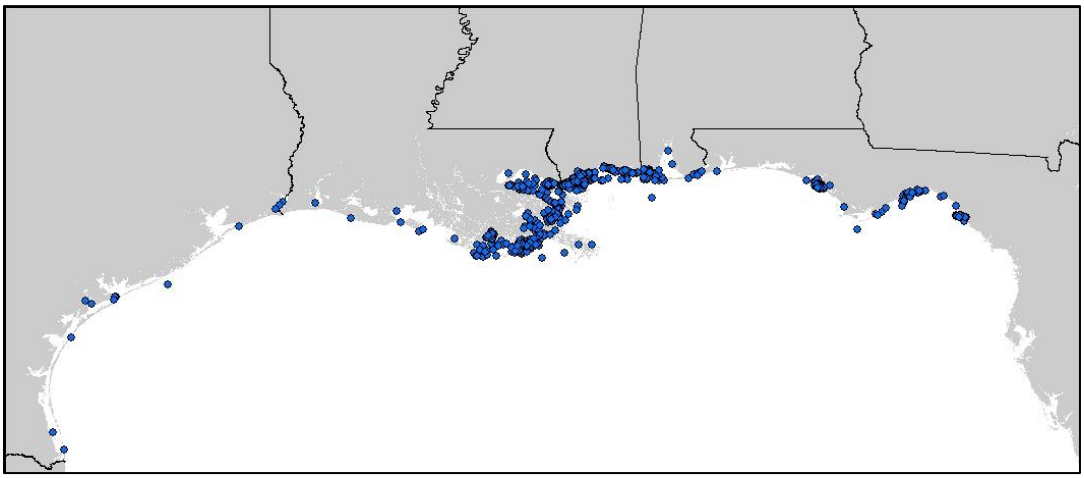

Figure 5. Recapture Locations

Locations of all verifiable recaptures. Each point represents a single recapture.

Table 4

State Tagging and Recapture Summary

State	# Tagged	# Recaptured	Recapture Rate
Texas	910	10	1%
Louisiana	5883	782	13%
Mississippi	1941	282	15%
Alabama	279	66	24%
Florida	3641	533	15%

Number of mature females tagged in each state, and the number of those from each state that were recaptured, with reporting rate.

Time between recapture and release, or time-at-liberty, ranged from 1 to 477 days, but the bulk (75%) were recaptured within 21 d of being tagged and 95% were recaptured within 69 d of being tagged (Figure 6). Median time-at-liberty for all recaptures was 11 days.

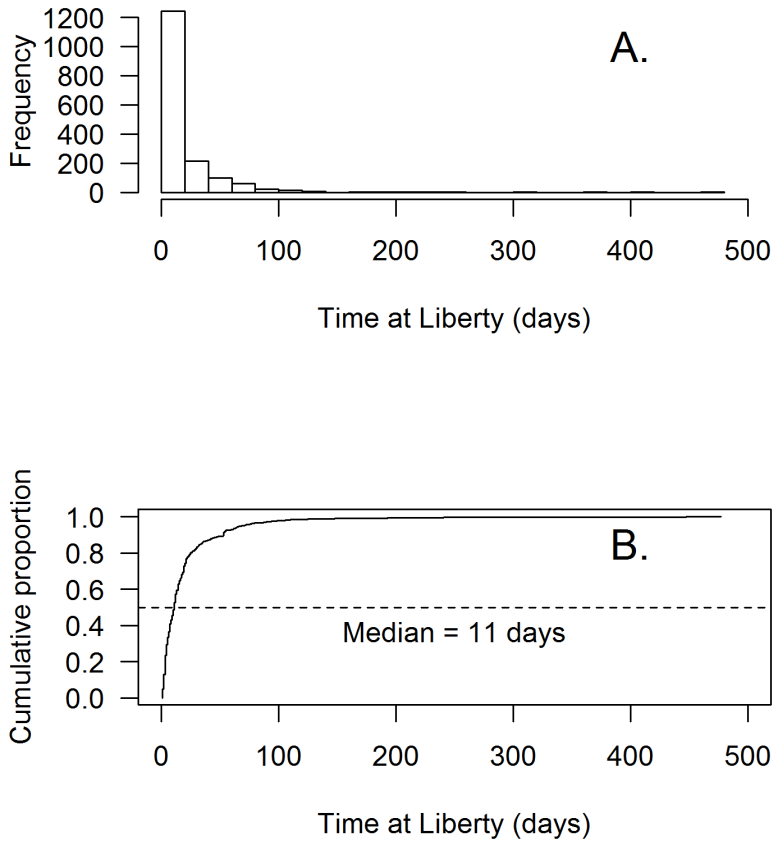

Figure 6. Time-at-Liberty Variability

Distribution of time at liberty measurements for recaptured crabs(A). Cumulative proportion of females that had been recaptured after (x) days (B).

Travel Distances

Least-cost distances for all recaptured females were estimated successfully at a 140m resolution. A visual inspection of shortest travel paths demonstrated satisfactory navigation around land barriers (Figure 9). Least-cost estimates of distances traveled ranged from 0 km for several females that were recaptured at the tagging location, to 440 km for a female that traveled around the Mississippi River Birdfoot delta from near Cat Island, MS to Cutoff, LA. As mentioned above, tagging effort was not spatially or temporally balanced. As a result, there are distinctly clustered areas of high tag releases.

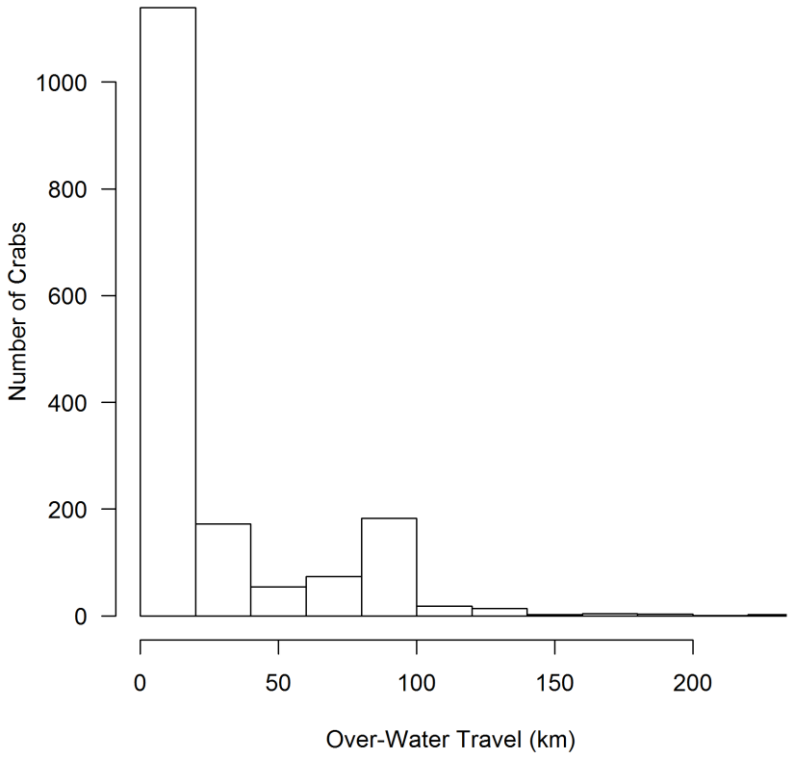

Figure 7. Travel Distance Frequencies

Estimated travel distances travelled. Distances represent the shortest-possible over-water distances (i.e., not crossing land barriers).

Comparisons to Euclidean distances showed a consistent trend of larger migration distance estimates for the least-cost path estimations (Figure 10). This is consistent with the rationale behind the method, and we believe this to be closer to reality than straight-line estimates. A paired Mann-Whitney rank sum test was performed to compare two distance measurements. Distances estimated using least-cost distances were significantly greater than Euclidean distances ($P < 0.0001$).

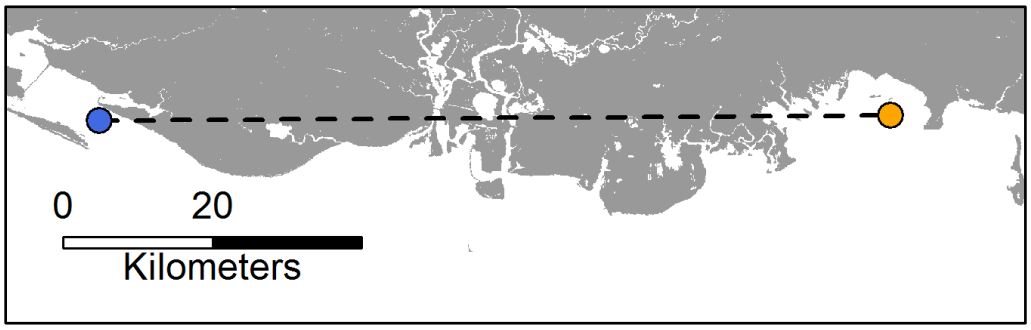

Figure 8. Example of Straight-Line Travel

Example of straight-line travel line (dashed black line). This female was tagged near marsh point in Ocean Springs, MS (blue point) and was recaptured in Grand Bay, AL (orange point).

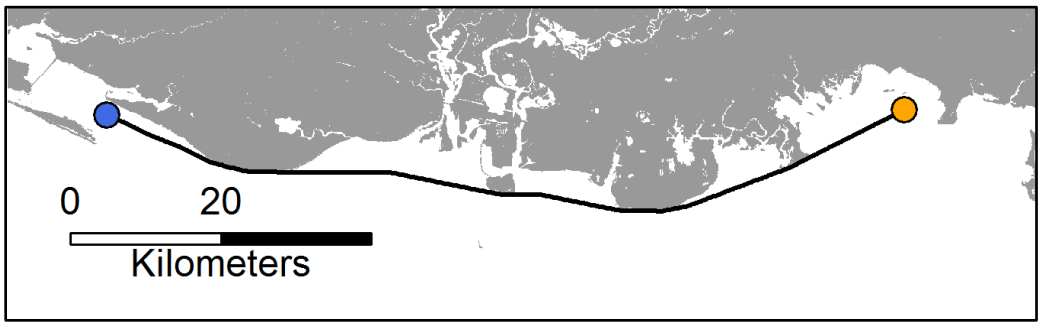

Figure 9. Example of Least-Cost Travel

Example of least-cost travel line (dashed black line). This female was tagged near marsh point in Ocean Springs, MS (blue point) and was recaptured in Grand Bay, AL (orange point).

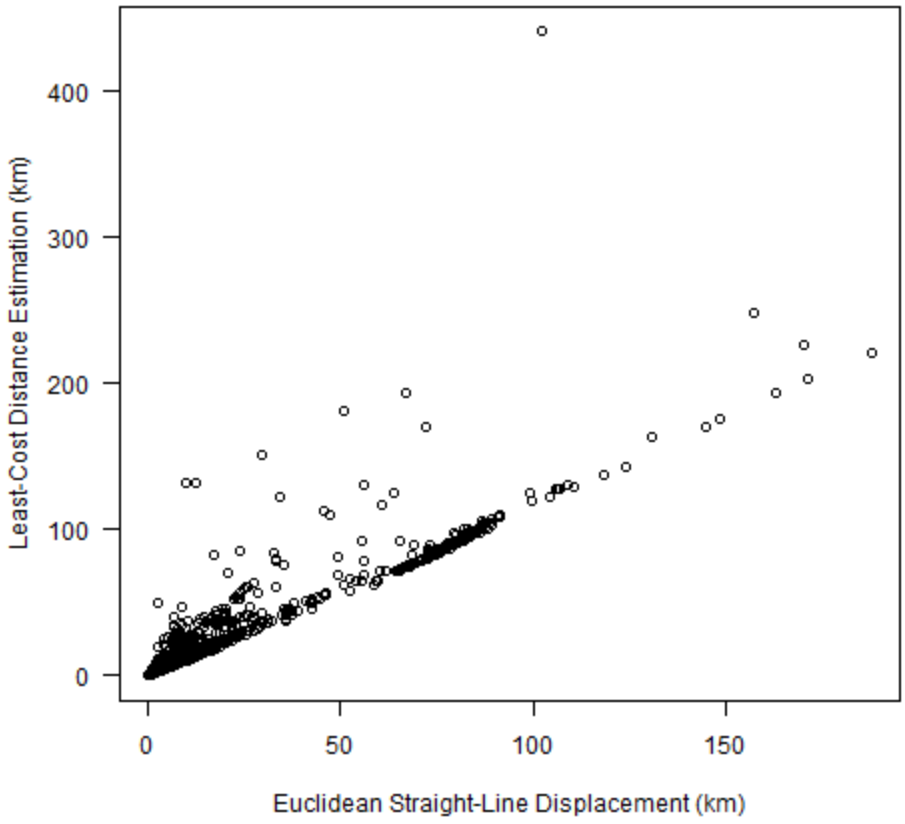

Figure 10. Travel Distance Comparison

Comparison of travel distance measurements (over-water least-cost distance vs. euclidian straight-line distance) for each crab.

Directionality of Movement

For each of the six regions tested, we rejected the null hypothesis of uniform directional travel, or random dispersal of crabs in each area. Female blue crabs tagged near Steinhatchee, FL in the Big Bend area exhibited both the largest mean displacement of 43.07 km, and the lowest variance around the mean direction estimate. The northwestern migration of these crabs is consistent with the previous tagging study conducted in that region, that showed a distinct northwestward migration up the Florida

peninsula but little movement west of Cape San Blas. Female crabs tagged in St. Andrew's Bay showed the least movement of any region in the study with a mean displacement of less than five kilometers.

Table 5

Rao's Spacing Test Summary

	Displacement 1–15 km			Displacement >15 km		
Region	N	Direction	*P*	N	Direction	*P*
Barataria Basin	251	218.05 (SW)	< 0.05	45	213.75 (SW)	< 0.05
Terrebonne Basin	112	109.50 (ESE)	< 0.05	18	113.32 (ESE)	>0.05
Mississippi Sound	535	93.22 (E)	< 0.05	140	83.52 (E)	< 0.05
North-central Gulf	65	256.57 (WSW)	< 0.05	21	255.86 (WSW)	< 0.05
Florida Panhandle	79	280.16 (W)	< 0.05	1	296.26 (WNW)	N/A
Big Bend Florida	401	295.83 (WNW)	< 0.05	231	298.45 (WNW)	< 0.05

Mean direction (degrees relative to N) travelled for each tagging region for crabs recaptured 1–15 km from the tagging location and >15 km from the tagging location. P values are from Rao's spacing test.

Table 6

Rayleigh Test Summary

Region	Displacement 1-15 km			Displacement >15 km		
	Direction	Angular Variance	*P*	Direction	Angular Variance	*P*
Barataria Basin	218.05 (SW)	82.47	< 0.05	213.75 (SW)	73.00	< 0.05
Terrebonne Basin	109.50 (ESE)	96.12	< 0.05	113.32 (ESE)	100.46	0.77
Mississippi Sound	93.22 (E)	97.80	0.15	83.52 (E)	28.97	< 0.05
North-central Gulf	256.57 (WSW)	83.24	< 0.05	255.86 (WSW)	40.78	< 0.05
Florida Panhandle	280.16 (W)	76.92	< 0.05	296.26 (WNW)	0	N/A
Big Bend Florida	295.83 (WNW)	99.68	< 0.05	298.45 (WNW)	3.38	< 0.05

Mean direction (degrees relative to N) travelled for each tagging region for crabs recaptured 1–15 km from the tagging location and >15 km from the tagging location. P values are from Rayleigh test statistic for unimodal travel direction.

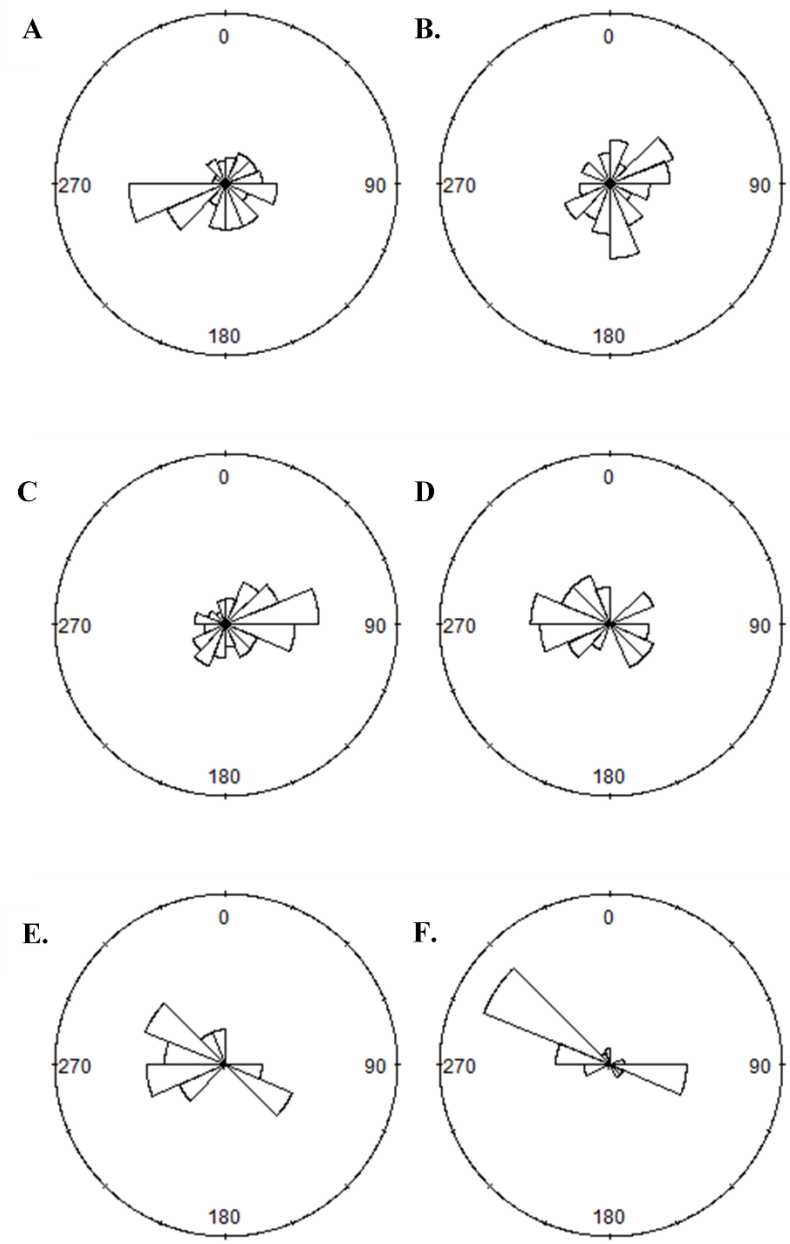

Figure 11. Rose Diagrams, Group 1

Rose diagrams (circular histograms) of the directions travelled by crabs in the Barataria (A.), Terrebonne (B.), Eastern Mississippi Sound (C.), Mobile Bay (D.), Florida panhandle (E.), and the Big Bend (F.) regions of the tagging study. Only crabs whose displacement was between 1 and 15 km were used for these plots.

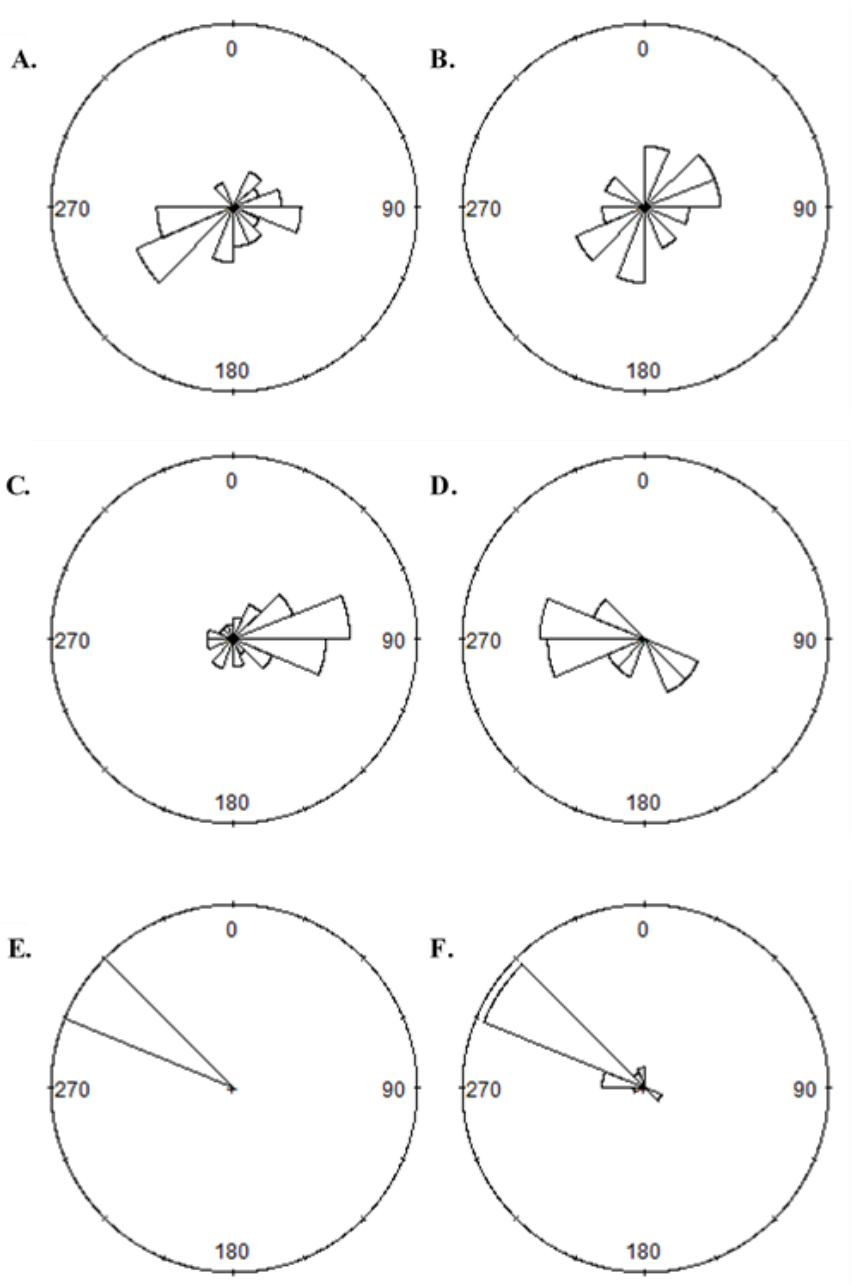

Figure 12. Rose Diagrams, Group 2

Rose diagrams of the directions travelled by crabs in the Barataria (A.), Terrebonne (B.), Eastern Mississippi Sound (C.), Mobile Bay (D.), Florida panhandle (E.), and the Big Bend (F.) regions of the tagging study for crabs whose displacement was > 15 km.

Travel Rates

Three markov chains were used for the estimation of each parameter in the bayesian model. This includes the shape and rate parameters for each gamma distribution, one for the global level, another for each season and basin respectively, and lastly for each region-season grouping. Each chain had a burn-in of 5000 iterations and was run for an additional 100,000 iterations post burn-in. All trace plots showed good mixing of the chains indicating good convergence. Gelman test statistics for each parameter were < 1.1, another indicator of model convergence. Posterior prediction of Gulf-wide travel rate distributions compared well with the distribution of the data collected. Median travel rate across the Gulf for all seasons was 0.27 km d^{-1} with 95% C.I. at 0.01 & 1.51 km d^{-1}.

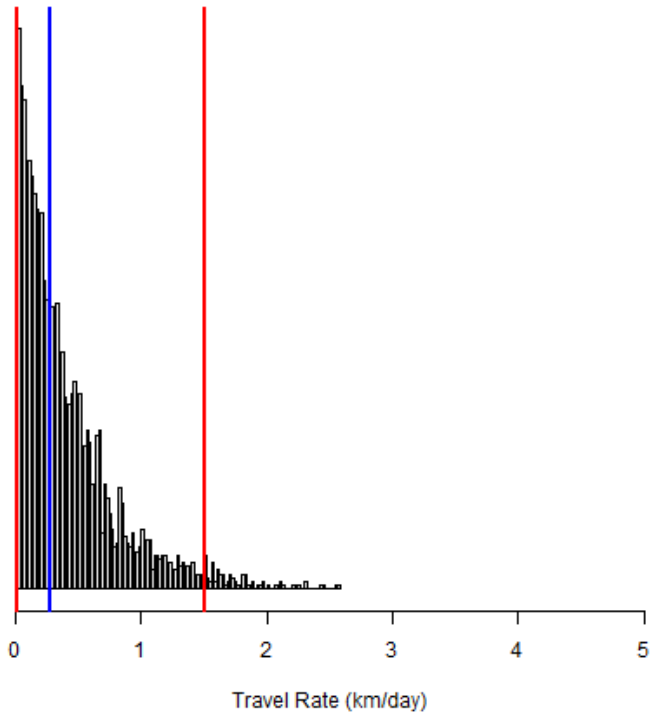

Figure 13. Gulf-Wide Travel Rate Posterior

Posterior estimates of travel rate across all regions and seasons with median estimate (blue), and 95% credibility intervals (red).

Posterior plots for season and basin showed indication that areas/seasons with large sample size like the Mississippi Sound region were well informed, given the tighter credibility intervals for each season. Regions lacking in data from specific seasons like the Big Bend, FL region, demonstrate how the hierarchical structure of the model can estimate probability distributions for seasons without data by using prior information from the same season information of other regions and the variance information from the spring season. As expected the credibility intervals are much wider for these estimates due to the larger uncertainty associated with the lower sample size. Travel rates with their credibility intervals for all season and basin combinations with available data was < 2 km d^{-1}. The summer months of June through August corresponded to the fastest travel rate estimates for each region, with the fall and winter periods corresponding to the lowest travel rate estimates.

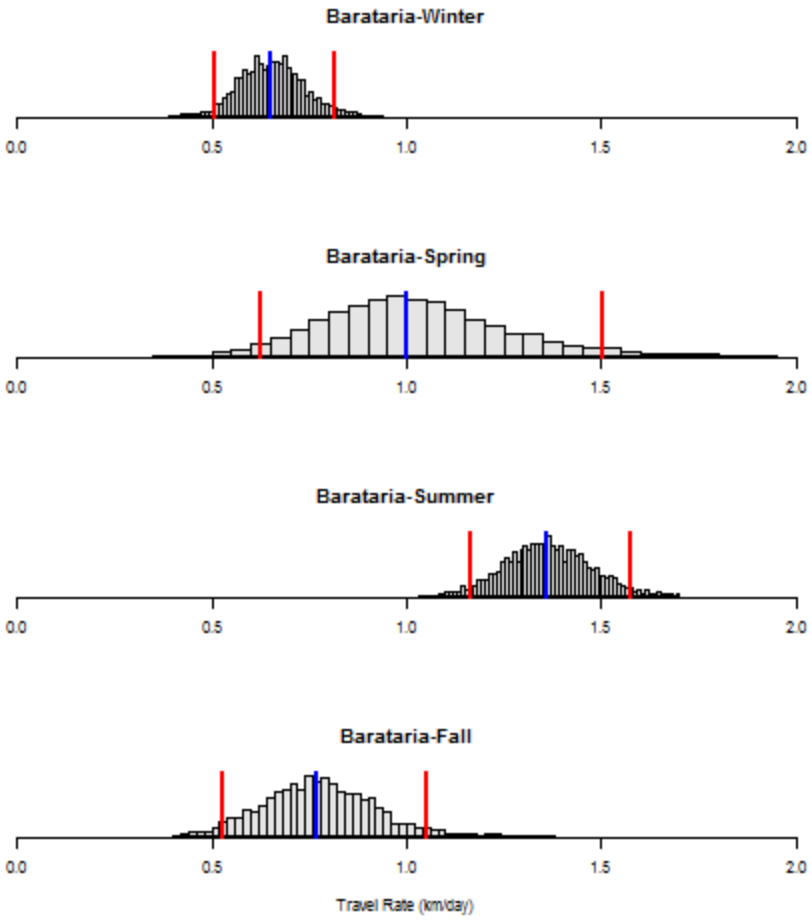

Figure 14. Barataria Travel Rate Posteriors

Estimated travel rates for the Barataria Bay region with median estimates (blue) and 95% credibility intervals (red) for each season.

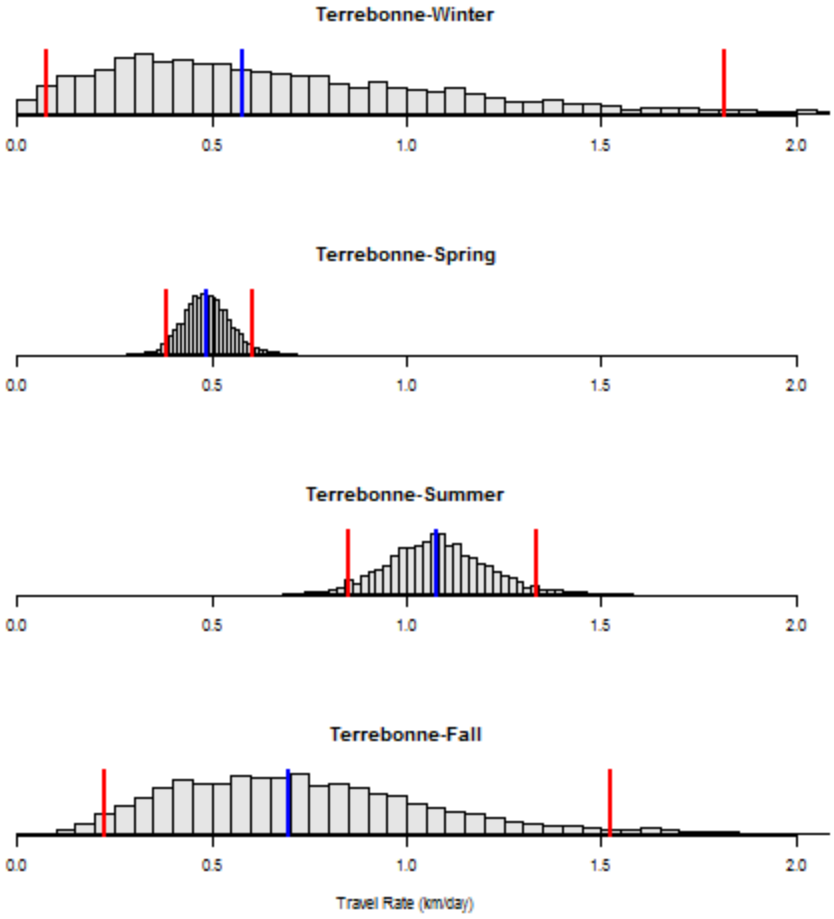

Figure 15. Terrebonne Travel Rate Posteriors

Estimated travel rates for the Terrebonne Bay region with median estimates (blue) and 95% credibility intervals (red) for each season.

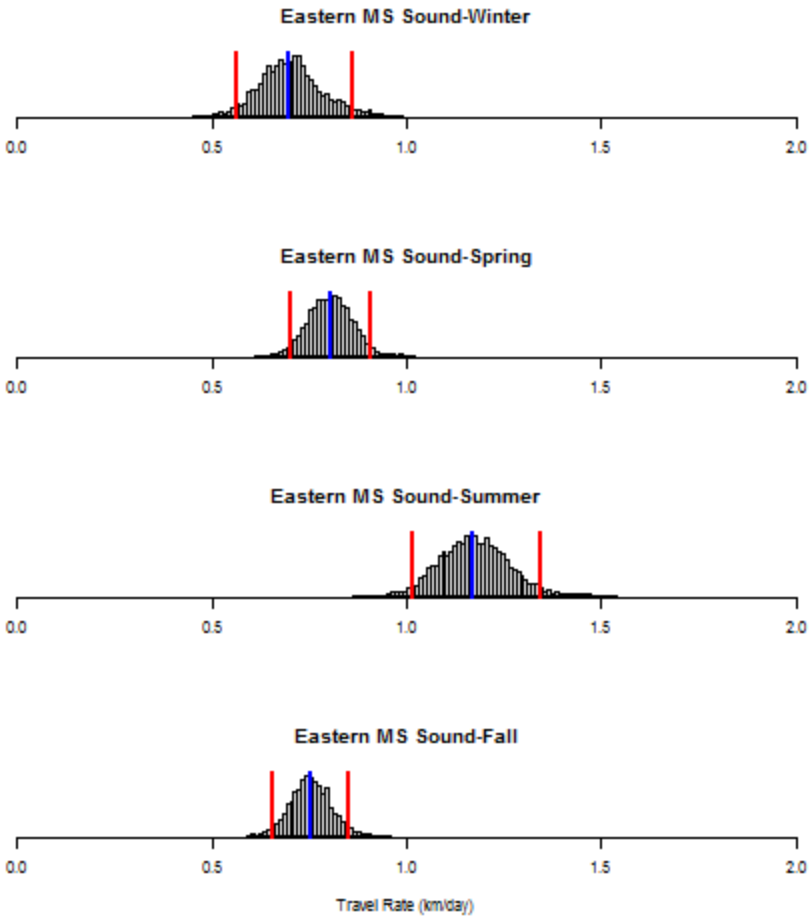

Figure 16. Mississippi Sound Travel Rate Posteriors

Estimated travel rates for the eastern Mississippi Sound region with median estimates (blue) and 95% credibility intervals (red) for each season.

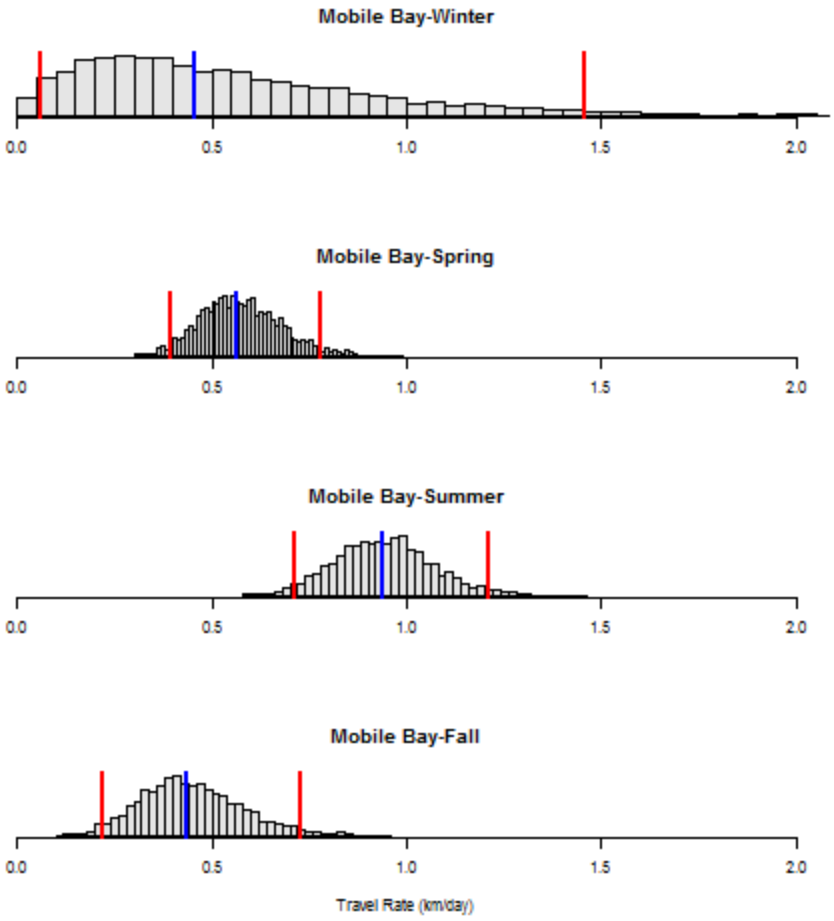

Figure 17. Mobile Bay Travel Rate Posteriors

Estimated travel rates for the Mobile Bay region with median estimates (blue) and 95% credibility intervals (red) for each season.

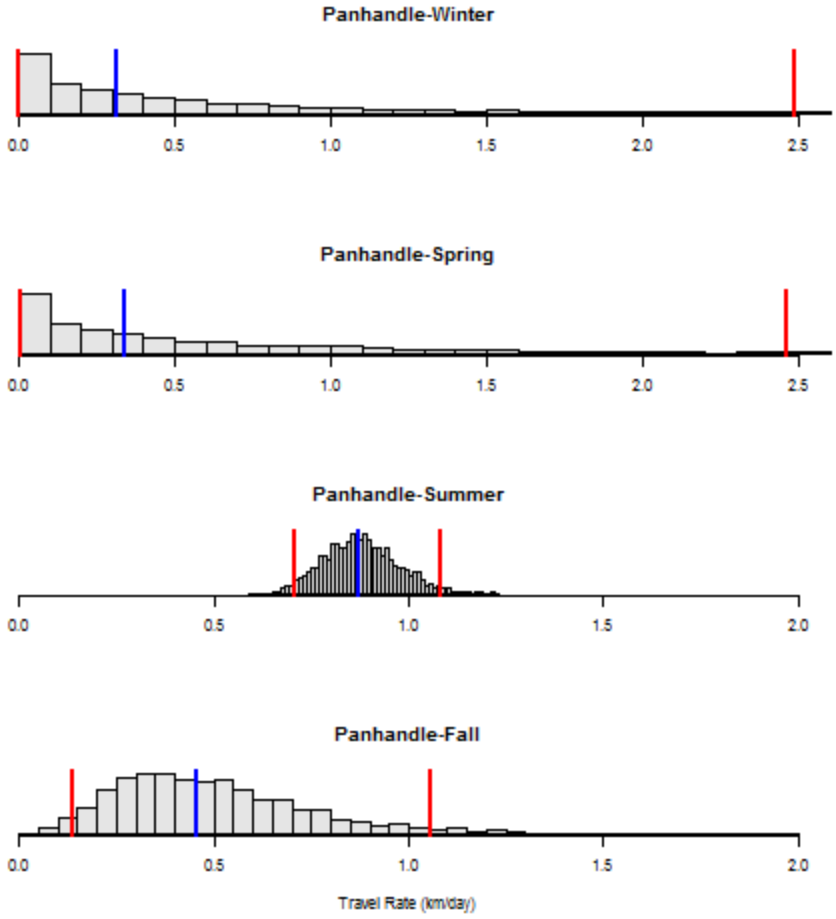

Figure 18. Panhandle Travel Rate Posteriors

Estimated travel rates for the Florida panhandle region with median estimates (blue) and 95% credibility intervals (red) for each season.

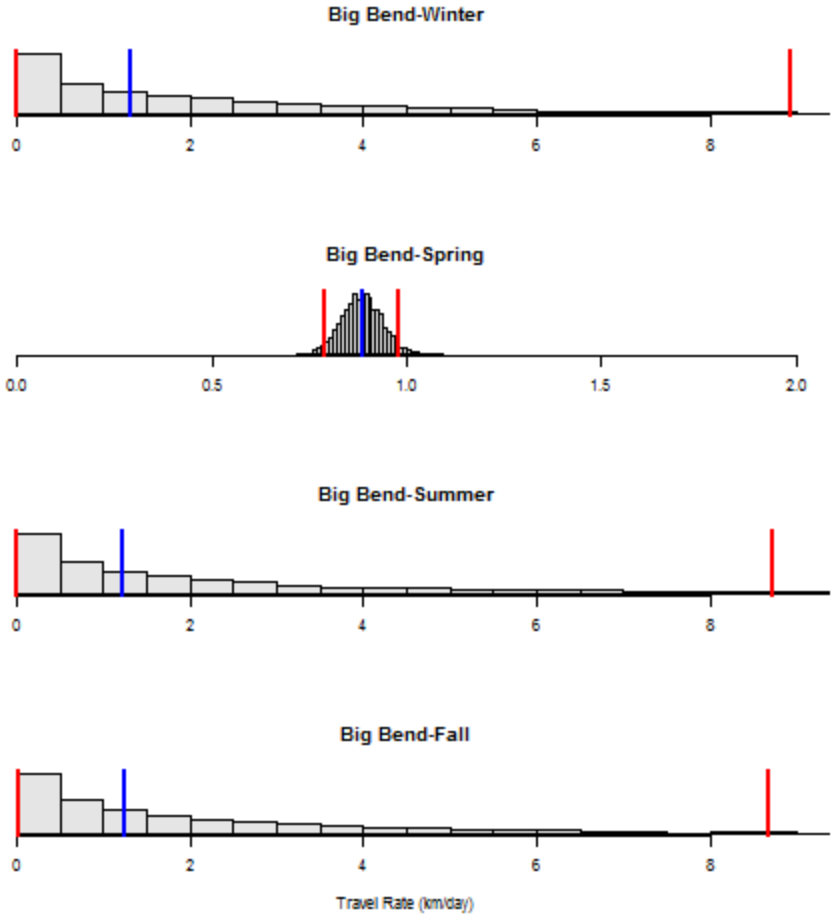

Figure 19. Big Bend Travel Rate Posteriors

Estimated travel rates for the Florida panhandle region with median estimates (blue) and 95% credibility intervals (red) for each season.

Table 7

Median Travel Rate Estimates

Region	Winter	Spring	Summer	Fall
Barataria	0.652 (0.508, 0.815)	0.999 (0.614, 1.50)	1.358 (1.162, 1.573)	0.770 (0.525, 1.053)
Terrebonne	0.577 (0.072, 1.817)	0.485 (0.3829, 0.6070)	1.074 (0.849, 1.330)	0.699 (0.223, 1.524)
MS Sound	0.698 (0.564, 0.863)	0.803 (0.699, 0.906)	1.171 (1.017, 1.346)	0.751 (0.657, 0.852)
Mobile Bay	0.457 (0.059, 1.457)	0.564 (0.394, 0.779)	0.939 (0.711, 1.208)	0 .437 (0.222, 0.729)
Panhandle	0.319 (0.002, 2.489)	0.338 (0.003, 2.465)	0.874 (0.708, 1.330)	0.455 (0.081, 1.054)
Big Bend	1.304 (0.008, 8.924)	0.889 (0.791, 0.978)	1.225 (0.009, 8.735)	0.770 (0.061, 8.661)

Median travel rates for each region. Numbers in parentheses represent 95% credibility intervals)

Seasonal Travel Rate Effect Sizes

When compared to the year round mean travel rate for all regions we saw significantly slower travel rates in the winter for the Mississippi Sound and Barataria regions. In the spring season the Terrebonne Bay and Mississippi Sound regions showed lower travel rates, but in the Big Bend region crabs were moving faster than the yearly average. In the summer season all regions were moving at above average rates except for Mississippi Sound which was moving below the overall mean, and the Big Bend area which showed no difference. In the fall season, only the Panhandle and Mississippi Sound regions showed a deviation from the overall yearly average with slower movement rates.

Table 8

Travel Rate Analysis of Variance

Region	Winter	Spring	Summer	Fall
Barataria	-0.47 (-0.75, -0.19)	0.03 (-0.54, 0.60)	0.21 (0.05, 0.37)	-0.23 (-0.65, 0.20)
Terrebonne	-0.46 (-1.95, 1.02)	-0.43 (-0.68, -0.18)	0.26 (0.01, 0.52)	-0.44 (-1.49, 0.61)
MS Sound	-0.24 (-0.45, -0.02)	-0.18 (-0.31, -0.06)	0.35 (0.20, 0.50)	-0.24 (-0.36, -0.12)
Mobile Bay	-0.49 (-2.36, 1.38)	-0.06 (-0.56, 0.43)	0.40 (0.02, 0.78)	-0.35 (-1.18, 0.48)
Panhandle	-0.33 (-1.03, 0.38)	-0.33 (-1.03, 0.38)	-0.46 (-0.52, -0.40)	-0.60 (-0.91, -0.40)
Big Bend	-0.33 (-2.36, 1.38)	0.22 (0.13, 0.31)	-0.33 (-2.23, 1.58)	-0.33 (-2.24, 1.58)

Median effect size estimates for each region. Numbers in parentheses represent 95% credibility intervals). A 95% credibility interval that does not cross 0 represents a significant deviation from the gulf-wide and year-long movement rate from this study.

Inter-jurisdictional Movements

Recaptures from neighboring states occurred frequently. Louisiana's female crabs frequently were recaptured in the neighboring waters of Mississippi (as expected, given proximity) but were also recaptured as far east as Florida. Crabs tagged on the Mississippi side of the same interface entered Louisiana water less frequently, however stock mixing did occur. Texas was the only state where mixing did not occur, but it is likely that with a larger sample the trend would occur there as well.

Table 9

Inter-Jurisdictional Travel Summary

		State Where Recapture Occurred				
		Texas	Louisiana	Mississippi	Alabama	Florida
Tagging State:	Texas	10	0	0	0	0
	Louisiana	1	709	65	5	2
	Mississippi	0	19	260	3	0
	Alabama	0	0	5	60	1
	Florida	0	0	0	0	532

Locations where females were recaptured (columns) for each state they were tagged in (rows).

DISCUSSION

The purpose of this study was to examine regional movement patterns of female blue crabs between estuaries and offshore waters of the Gulf of Mexico, using a large-scale mark-recapture study.

Recapture rates were similar for crabs tagged in Louisiana, Mississippi, and Florida, ranging from 13–15%. These reporting rates are within the range of reporting rates of previously conducted tagging studies (11.6%: Aguilar et al., 2005; 0.3–20%: Medici et al., 2006; 5–21%: Turner et al., 2003; 17.5–39.7%: Darnell and Kemberling, In Press). Crabs tagged in Alabama had a slightly higher recapture rate of 24% while crabs tagged in Texas had a substantially lower recapture rate of 1%. The factors driving Alabama's high recapture rate are unclear. Alabama reported < 2 million pounds of blue crab landings in 2016, nearly 1/20th the landings reported by Louisiana (~40 million). We did not anticipate Alabama to have such a high recapture rate for a state not known to support the level of fishing pressure that other Gulf states sustain. This high recapture rate could reflect greater cooperation by Alabama crabbers relative to those in other states. The low recapture rate for crabs tagged in Texas could be due to two factors: (1) the method by which crabs were tagged, and (2) lower fishing pressure relative to the other four Gulf states. Crabs in Texas were tagged entirely during fishery-independent surveys, characterized by releases of small numbers (typically <5) of tagged crabs at any given location, with tagging locations spread out across all bay systems due to the randomized design of the survey program. In contrast, tagging in the other four states was primarily fishery-dependent, with most crabs tagged on commercial crab boats, resulting

in releases of large numbers of tagged crabs in relatively small areas, and in areas where commercial crabbers regularly operate. We we were able to evaluate the effect of taggin methodology on recapture rates by comparing recapture rates for (1) crabs tagged in Texas through fishery-independent surveys: 1% recapture rate, (2) crabs tagged in Louisiana through fishery-independent surveys: 4.9% recapture rate, and (3) crabs tagged in Louisiana through fishery-dependent methods: 13.6% recapture rate. Louisiana was used for comparison because of large numbers of crabs tagged using both fishery-independent and fishery-dependent methods. Similar recapture rates for Texas and Louisiana considering only crabs tagged in fishery-independent surveys suggest that tagging methodology (fishery-dependent vs. fishery-independent) can influence recapture rates. The low recapture rate in Texas may also be due to lower commercial fishing pressure in Texas, relative to the other states. The vast majority (87.3%) of recaptures in all areas were reported by commercial crabbers. While Texas has a commercial crab fishery, landings (2,263 metric tons in 2016) are low relative to the length of the coastline and are at low levels relative to historical highs in the 1980's, likely reflecting low fishing pressure throughout the state.

The blue crabs tagged in this study travelled a combined 42,700 kilometers by our least-cost estimation, with marathon travelers crossing hundreds of kilometers across jurisdictional boundaries. Though our largest estimated travel rate could not compare to the travel of a female tagged in the Chesapeake Bay that was recaptured in Florida (1040 km) (Aguilar et al. 2005), our tagging study confirms that blue crabs are quite capable of traveling long distances during the spawning migration. Our decision to estimate travel

distances around land barriers resulted in longer travel estimates and consequently faster travel rates. Many previous studies use straight-line displacement to estimate distance travelled. While this may work on a rough scale for a largely linear estuary like the Chesapeake Bay, it becomes less applicable along a complex shoreline like that of the Gulf of Mexico. As our tagging data showed, females readily travelled beyond their estuary systems navigating around migratory barriers. In areas like the Chesapeake Bay where there is a clear migratory corridor the underestimation of travel is likely less of an issue, but with Louisiana's rapidly fragmenting coastline, and with a large portion of our tagging locations conducted in small inland waterways we felt that straight-line travel distances would not accurately reflect the routes taken.

Movements of female crabs from each region were shown to not follow a uniform circular distribution of dispersal direction. All regions except the Mississippi Sound region showed a unimodal direction of travel, and for crabs in that region that travelled >15km there was a significant Eastward direction of travel. Recapture locations collected from females tagged in Florida waters confirmed the previous tagging studies that recorded a northward migration for females south of Apalachicola. In stark contrast to the large distances we tracked for crabs in the Big Bend area, those tagged in the panhandle region rarely traveled beyond the St. Andrews Bay area. Further research is needed to determine why females tagged near Steinhatchee, FL in the Big Bend region would travel so consistently in one direction, while crabs tagged in the panhandle under similar water conditions moved very little. Salinity, temperature, and DO measurements recorded in both areas at the times of tagging showed similar measurements, but only represent a

single snapshot of conditions and may miss a larger spatial trend. The GSMFC in the past has suggested a division of the Gulf of Mexico's blue crab spawning populations into an Eastern and Western population, dividing Florida just west of Apalachicola Bay based on the results of a previous tagging study (Steele, 1991), which found that females tagged along the Gulf coast of peninsular Florida moved northwest, but did not cross Cape San Blas. The prevailing idea at that time was that the freshwater outflow associated with Apalachicola Bay was a sufficient deterrent to female blue crabs migrating westward, and that the mixing of adult populations between the two areas was limited. Our tagging data confirms the patterns observed previously but does not identify any causal factors that are driving those patterns. If indeed the major deterrent for migratory females was the relative drop in salinity freshwater outflow, then Mobile Bay and the Mississippi River should act similarly in fragmenting the gulf blue crab population(s). We had a single female blue crab cross the Mississippi River Birdfoot Delta, and several females traverse the mouth of Mobile Bay from West to East. Our tagging study does not conclusively show that these hydrological features act as barriers for migrating females, which makes the polarizing differences between both regions in Florida so interesting.

Female migration towards the higher salinity waters at the mouths of their home bay or estuarine systems occurred as we expected based on previous studies, however their movements beyond these areas are still poorly understood. Crabs tagged in each basin of Louisiana showed a clear outward migration, with a prevailing course that typically pointed straight outward from each particular basin. The rationale that they are cueing primarily on salinity and turbidity changes begins to deteriorate when you have

females crossing both the Pearl River and Mobile Bay, two freshwater outflows that should deter females following those cues. Overall, the recapture information collected confirms that adult blue crabs in the Gulf of Mexico are regularly mixing, making it nearly impossible that the state populations are independent of one another, particularly when one remembers the larval dispersal phase of 30-50 days. Females tagged between the Mississippi River and Perdido Bay showed no structural separation, with high mixing occurring between each state. Mississippi's nearshore waters were shown to be supporting visitors from both neighboring states, and females from Louisiana traveled as far as Florida. Our tagging coverage in Mississippi was primarily conducted in waters beyond the mouths of Bay St. Louis, Biloxi Bay, and the Pascagoula River, so we are limited on the certainty that we have that the crabs we tagged were indeed Mississippi natives. Future work investigating how mixed the populations in this region are would be interesting, as Mississippi's blue crab population is almost certainly dependent on the spawning stock of its neighbors, as adults from both neighboring states were shown to actively spawn within their jurisdictional boundaries. This leaves their fishery's sustainability in the hands of other state management policies. By all estimates obtained in this study, there is no case to be made for isolated state stocks of independently sustaining blue crab populations.

The travel rate estimates we were able to obtain were similar to the patterns we expected, with higher travel rates in the summer months, when crab metabolism is higher, with less movement in the winter, when metabolism is lower. Movement rates observed here are in line with what has been observed in other areas, although rates are difficult to

compare given differences in the methods for calculating travel distances and measure of central tendency used. Crabs making the analogous spawning migrations in the Chesapeake Bay were estimated to travel at a mean travel rate of 3.3 ± 0.35 km day^{-1} (Aguilar, 2005), although they considered only crabs captured >25 km from the tagging site. In the present study, crabs that were captured >25 km from the tagging site had a mean travel rate of 4.30 ± 3.69 km day^{-1}, but as mentioned previously the mean rate may not reflect the central tendency as well as the median (0.45 km d^{-1} for crabs traveling >25 km) due to the right-skew in the data caused by several exceptionally high travel rates. Recently-molted crabs tagged in North Carolina (which had not yet necessarily begun the spawning migration) were estimated to travel 0.5 ± 0.05 km d^{-1} (mean ± SE, median = 0.11 km d^{-1}) when considering all crabs tagged, or 1.6 ± 0.32 km d^{-1} (median = 0.91 km d^{-1}) for crabs that traveled >25 km from the tagging location (Darnell & Kemberling, in *Press*). Variation in travel rates is likely to vary strongly with the degree of current and tidal forcing in the area, as they are actively changing their swimming behaviors through ETT. A much more accurate way of determining migratory rates is to actively track females as they migrate, as has been done in North Carolina (Carr et al. 2004). Movement rates estimated here are lower than those observed by Carr et al. (2004), who observed movement rates averaging 5.4 km d^{-1}. Carr et al. (2004) were tracking females in a strongly-tidal estuary (Beaufort Inlet, NC), and over a short time period (<48 h). In contrast, the goal of the present study was to gain insight into long-term movement patterns of spawning crabs in the Gulf of Mexico, and our movement rates thus reflect

integrated movement rates over the full period during which the tagged crab was at liberty.

All travel rate estimates from mark-recapture studies (including the present study) are limited in the sense that they were drawn almost entirely from paired point estimates assuming constant travel from point A to point B. This is almost certainly not the case for most of the females recaptured. Swimming behavior among mature female blue crabs has been shown in other areas to vary with local depth and flow regimes while controlling for the tidal cycle (Darnell et al., 2012), and in other areas scientists have been able to identify forage and staging habitats where females may spend prolonged periods (Eggleston et al., 2009). Self-reporting of times and locations of recapture events adds another layer error as descriptive locations may not be accurate and GPS locations are assumed true and honest. By using the hierarchical bootstrapping structure, we are assuming to some degree that temporal and spatial correlation be consistent enough to draw estimates for areas and seasons from which we did not have samples. Seasonal posteriors for the Big Bend area showed the wide uncertainty for Winter, Summer, and Fall because caused by the lack of sampling in those periods. The median estimates for those months are comparatively high for the season because the large number of samples we have for spring suggest a regional estimate larger than the seasonal posterior. Any inferences made in this study on travel rates are limited by the study design as a mark-recapture study with unequal spatial and temporal sampling. Though we were able to make estimates in this way, there is a degree of subjectivity in the setting of priors, particularly in cases where there is little data. Though we selected diffuse priors for

bootstrapping, and the resulting wide credibility intervals reflect it, there is the option of using informed priors using travel rate estimates from previous studies. The choice to use diffuse priors was made to reflect the level of uncertainty around the estimates we had collected, while still allowing us to still make statements on travel rates that differences in sampling effort and the recapture data collected would otherwise have prevented. A mark recapture study conducted the way this study was conducted is simply not designed to capture the minute details of the timing and travel speeds of migratory females. If there is one thing our posterior estimates show, it is that they could benefit from additional data, and that they should be regarded as reference points rather than biological truths.

One of the biggest limitations of this study, and any mark-recapture study, is the dependency on recapture information to prove state-space relationships. One of the biggest questions for this study is where crabs are moving once offshore, and where offshore females are originating. We did not get the recapture on these crabs like we had hoped. Much of the commercial fishing pressure, which accounted for the majority of our information obtained, is concentrated in inshore areas. Consequently, most of the information we collected is spatially biased in this way. Between that and the low reporting rate from the shrimping industry, it was just not likely that a female would be recaptured once it had moved offshore.

Blue crabs in the Gulf of Mexico are not managed on a spatial scale that reflects their adult and larval dispersal scales, limiting the effectiveness of management actions. The spawning stock has been shown to regularly travel beyond arbitrary management boundaries, releasing larvae that disperse even further. The consistent northwestward

migration of females along Florida's west coast, and the open mixing of state populations in the Northern Gulf of Mexico between Lake Pontchartrain and Perdido Bay should be considered as they likely contribute to considerable emigration of adults, and the larvae they release. Travel rates across the Gulf confirm that females are non-stationary as they are in the Atlantic, and that their movement rate varies by season and local environmental factors. These variations should be considered when making decisions like seasonal closures aimed to protect the spawning stock from fishing pressure. This work showed that females in most of our six regions travelled the most during the warmer months of the year. This could be due to a change in their behavior due to a seaward spawning migration, or an increase in metabolic function with warmer temperatures. Management actions like the recent seasonal closures in Louisiana during the spring are designed to give females a period to safely migrate seaward. The data from this study suggests a summer closure would more closely match the period of peak female movement, potentially allowing for a greater escapement rate of the female spawning stock.

CHAPTER III - DISTRIBUTION, ABUNDANCE, AND REPRODUCTIVE CONTRIBUTION OF SPAWNING FEMALE BLUE CRABS IN OFFSHORE WATERS OF THE GULF OF MEXICO

INTRODUCTION

In the period following their terminal molt, female blue crabs mate and store the sperm necessary for their life-long reproductive contribution (Dickinson et al., 2006). Blue crabs are a highly fecund species, and despite only mating once in their lives, they produce large broods of several million larvae at a time (Darnell et al., 2009). After mating, the females must travel to spawning grounds of sufficiently high salinity to spawn, producing multiple subsequent broods from that singular mating window (Millikin & Williams, 1984). Each brood of larvae is released into the water columns as zoeae which disperse through advection of the winds and currents for 30–50 days before their eventual recruitment and reinvasion of coastal habitat as megalopae and juveniles soon after (Hines et al., 1987). Spawning female blue crabs are often found in large numbers at or near the mouths of estuaries, yet the spawning migration does not stop at the edge of the estuaries. Female blue crabs continue migrating throughout their reproductive period (Darnell et al. 2012, Hench et al. 2012), and continuing to move into offshore waters. Actively spawning mature female blue crabs have been collected as far as 150 km from land in the Gulf of Mexico, and females are commonly sampled in fisheries independent trawl surveys well beyond the mouths of bays or estuaries where they are typically found (GSMFC, unpublished data).

As a state-managed species, indices of abundance and fecundity estimates for blue crabs are formed through various survey methods conducted within state waters. Each state in the Gulf of Mexico maintains jurisdiction over its inshore waters and the surrounding offshore environment up to nine miles from the coast. However, blue crabs are most abundant within or near the inshore marsh and estuarine habitats, and as such there is little incentive for state management agencies to survey offshore habitats occupied by less dense crab populations (Hines et al., 1987). While blue crabs are less densely populated offshore, there is much more offshore habitat relative to the inshore habitats they are most known for occupying, and recent work done in the South Atlantic bite suggests this often-overlooked offshore population may contribute substantially to the spawning stock of the region (Ogburn & Habegger, 2015). Additional research in the Gulf of Mexico has shown high densities of female blue crabs off the coast of Louisiana on the Ship, Tiger, and Trinity Shoal Complex, which are thought to be important foraging grounds (Gelpi, 2009). Off the coast of Texas, female blue crab offshore abundances were shown to be explained best by proximity to the mouths of Texas' bay passes, with salinity and temperature also being consistent environmental covariates (Andersen et al., 2017). However, the data used in their study was collected as part of Texas' fisheries independent surveying, which only samples within 10 km of the passes, and areas further offshore were not sampled. They also suggest that the decline in Gulf-wide blue crab populations may be attributed to a multi-decadal decline in spawning stock, of which the offshore proportion has been largely overlooked by traditional stock assessment measures.

To assess the importance of offshore female blue crabs with regards to the overall spawning stock biomass in the Gulf of Mexico, females were collected during the 2017 summer and fall Southeast Area Monitoring and Assessment Program (SEAMAP) groundfish surveys to conduct reproductive analyses and assess the overall health of females occupying these habitats. Spatial and temporal trends in offshore blue crab catch data were then assessed using the SEAMAP dataset, to identify predictors of offshore abundances and identify regions of important spawning habitat.

METHODS

Southeast Area Monitoring and Assessment Program

The Southeast Area Monitoring and Assessment Program (SEAMAP) is a state/federal/university partnership for the collection of fishery-independent data in the southeastern U.S. The SEAMAP-Gulf of Mexico program began in 1981 and conducts a number of fishery-independent survey programs including groundfish surveys, plankton surveys, reef fish surveys, and longline surveys. Trawl sampling conducted for the SEAMAP groundfish surveys is conducted off the coast of each of the five Gulf states, up to 200 nm from shore, twice a year each summer (June–July) and fall (October–November). The study area is divided into 21 statistical zones based off the National Marine Fisheries Service's gulf shrimp landing statistical zones (Figure 20.). These are further divided for SEAMAP into two depth zones, 2–20 fathoms and 21–60 fathoms, with the exception of statistical zones 18-21 off the coast of Texas where depth limitations of the RV Oregon II prevent sampling in shallow water areas.

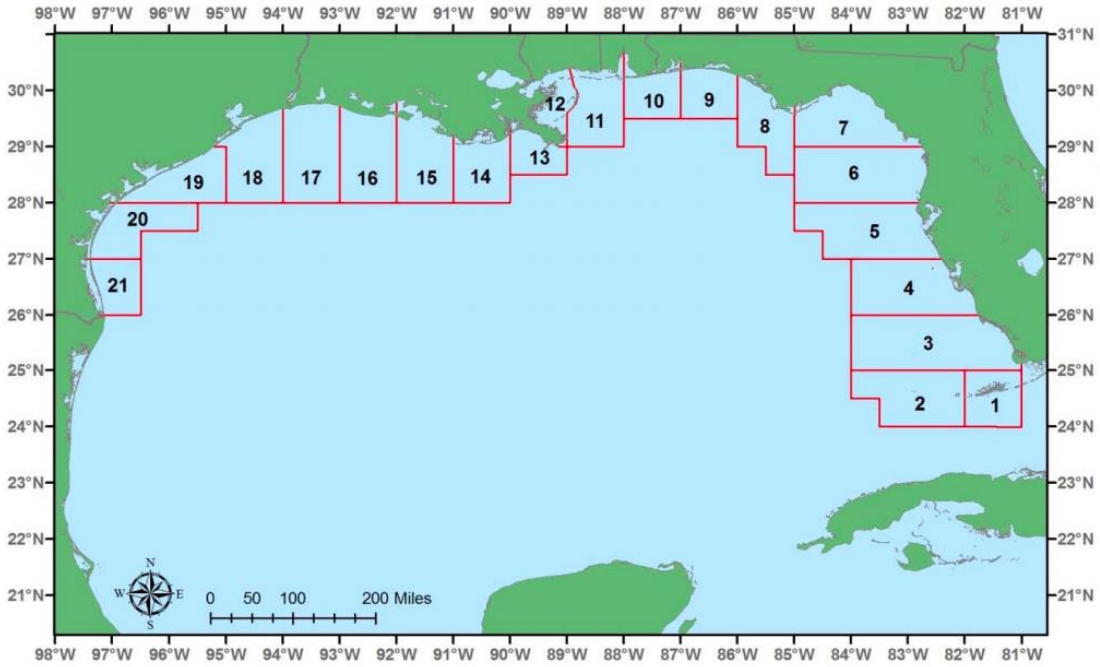

Figure 20. SEAMAP Statistical Zones

National Marine Fisheries Service gulf shrimp landings zones for the Gulf of Mexico adopted as the statistical zones for SEAMAP.

Sampling stations are selected within each statistical/depth zone using probability sampling in which the probability of a given bottom type being sampled (and thus the total number of samples in that bottom type) is proportional to its geographic area. At each trawl station a CTD is lowered to record a suite of environmental variables including chlorophyll-a, dissolved oxygen, salinity, and temperature. Each station is then sampled using a 40' trawl (1.63 inch stretched mesh size), towed for thirty minutes. The geographic locations, start and end times, and tow speed are recorded for each tow. The catch is then weighed and measured in its entirety for select species, and as subsamples for non-select species (which include blue crabs). For non-select species the total

abundance of the catch is recorded. The lengths of up to twenty individuals are then recorded, along with the weight and sex of every fifth organism in the sample.

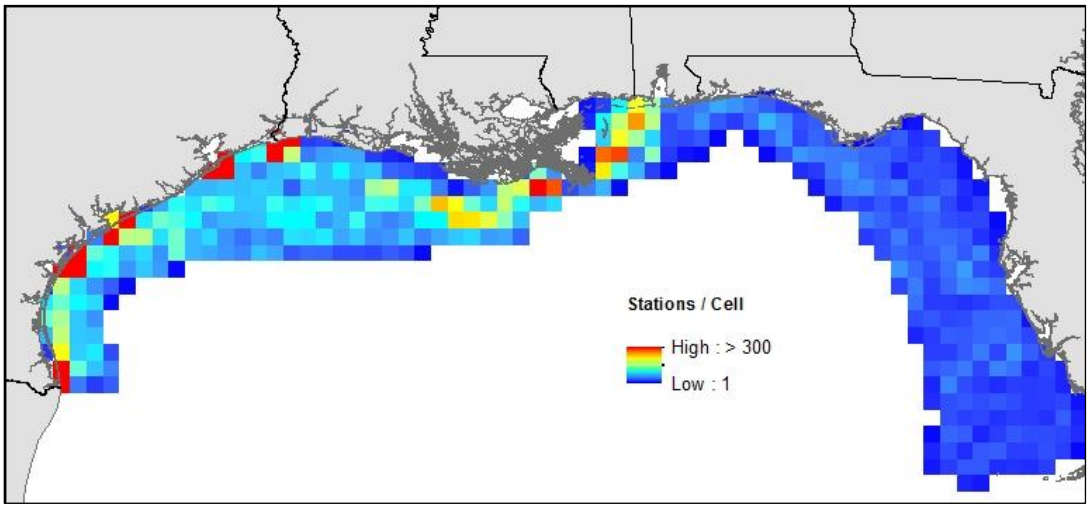

Figure 21. SEAMAP Station Sampling Frequencies 2001-2016

SEAMAP sampling stations aggregated into 0.25° x 0.25° grid cells for the years of 2001-2016. Symbol color represents number of samples that occurred in the cell with cooler colors representing cells with fewer stations and red representing cells with the highest number of sampling stations.

Condition and Reproductive Output of Spawning Females Collected Offshore

Mature female blue crabs were collected the 2017 SEAMAP summer and fall groundfish trawl survey. Up to five mature females were haphazardly selected from each trawl sample, individually bagged, and frozen, for a total of 114 females collected during the summer survey and 11 females collected during the fall survey. Frozen crabs were returned to the Gulf Coast Research Laboratory (GCRL) in Ocean Springs, MS for analysis.

Prior to analyses, crabs were thawed in the refrigerator. Carapace width (measured as the distance between the tips of the lateral spines), short carapace width (distance between bases of each lateral spine), total crab mass, molt stage (Table 1.),

reproductive stage (Table 2.), and any abnormality in appearance (missing legs or excessive fouling) were recorded for each crab. Females without egg masses were inspected for egg-mass remnants on the pleopods, and their gills were inspected for parasitic worms, each of which provides evidence of prior spawning.

Following external inspections, the egg mass was removed from each ovigerous female by careful separating the egg mass from the pleopods, and the weight of the egg mass was measured. A <1 g subsample (typically 500–1000 eggs) was then removed and weighed, and the total number of eggs in the subsample was counted using a stereoscopic microscope. The developmental stage for each egg sample was then determined visually using the scale of DeVries et al. (1983), and the percentage of embryos developing normally was visually assessed based on 20 eggs chosen at random from the subsample. Egg diameter for 20 normally developing eggs was determined by measuring along the long axis and its perpendicular axis using a compound microscope. The mean measurement for each was calculated and used as the egg diameter, and later for egg volume conversion.

Each female was also given an internal inspection for parasite presence and reproductive condition. Gills were inspected for the presence of the parasitic gooseneck barnacle *Octolasmis muelleri,* and for the parasitic nemertean worm *Carcinonemertes carcinophila*. Spermathecae, the paired sperm storage organs, were located to determine if she had recently mated. A female was determined to have recently mated if her spermathecae organs had not yet reabsorbed, maintaining a large size, firm texture, and pink coloration at this stage (Ogburn & Habegger, 2015). Because females only mate once in their lifetime, following their terminal molt, this is an indication that a female

moved offshore soon after her mating, or that mating occurred in an offshore environment. Each female was determined to be spawning capable if she showed developing ovaries or actively carried an egg mass. Females without healthy appearing ovaries were determined to be finished spawning for the season.

Fecundity of females collected offshore was modeled separately for the predictor of carapace width using a generalized linear model with an identity link function, and a generalized linear model using the log link function. Both models were done in a Bayesian framework to obtain median and 95% credibility estimates of model parameters (slope and intercept) using the JAGS package (Hornik et al., 2003) in the R statistical environment (R Core Team 2016). Model prediction was assessed using using deviance information criterion (DIC). The DIC is used similarly to AIC, and the more diffuse the priors are, the more the DIC approximates to the AIC. Bayesian p-values were used for model fitting diagnostics, in addition to the visual inspection of residuals. Bayesian p-values reflect the tendency of a model to over or underestimate data, bayesian-p values range from 0 for a model that underestimates 100% of the observed data, to 1 for a model that overestimates all observed data. Bayesian p-values around 0.5 show a lack of bias towards either over or underestimation.

Distribution and Abundance of Spawning Female Blue Crabs in Offshore Waters from Historical SEAMAP Data

Historical SEAMAP groundfish survey data was made available by the Gulf States Marine Fisheries Commission and is complete for the years 1982–2017. Initial exploratory data analyses revealed that blue crab catch per unit effort (CPUE) and

associated variance in CPUE declined substantially after 1990. Other scientists in the region have expressed concern that during the early years of the SEAMAP surveys, *Callinectes sapidus* and *Callinectes similis* may not have been distinguished, which could lead to this decrease in both mean and variance. To account for possible mis-identifications during the early years of the surveys, only data from 2001–2016 were used for all further analyses. To look investigate spatial trends in the dataset that persist over the study period, station catch information was aggregated into 0.25° x 0.25° grid cells using the point to raster tool in ArcMap. The resolution for grid aggregation was chosen arbitrarily to maintain a continuous surface for visualization purposes, and not used for any further analyses. This was done for both the summer and fall sampling periods to investigate any spatial trends that may be present in only one sampling period.

Blue crab catch on SEAMAP's groundfish survey was modelled with a seasonal random intercept for summer and fall sampling periods to account for short term temporal correlation among seasons. To account for the considerable number of zeros in the catch data, blue crab abundance was predicted using a negative binomial generalized linear mixed model with the environmental covariates of bottom dissolved oxygen, surface chlorophyll-a measurements, bottom temperature, and bottom salinity. Temporal variation was incorporated through a small-scale seasonal random effect, and at a large-scale through a yearly random effect in the model. Dominant bottom cover type was incorporated as another random effect using data from the usSEABED database (Buczkowski et al., 2006), with the dominant bottom cover types binned as four levels of progressively larger grain size (mud, sand, gravel, and rock). Model candidates were compared using Deviance Information Criterion (DIC). All model candidates were

implemented using R-INLA and the most parsimonious of those candidates then incorporated spatial autocorrelation structure using an SPDE model (Lindgren & Rue, 2015). All continuous variable covariates were scaled to aid in computation and to detect effect sizes.

Final Model Candidate Structure

Blue crab abundance (CA) at site i for years with an E.I. of j, is negative binomially distributed around the mean of site i and an E.I. of j with dispersion parameter k:

$$\mathrm{CA} \sim NB(\mu_{\mathrm{ij}}, k)$$

The expected crab abundance at site i for E.I. of j is μ_{ij}, and the variance is $\mu_{\mathrm{ij}} + \frac{\mu_{\mathrm{ij}}^2}{\mathrm{k}}$

$$E(CA_{\mathrm{ij}}) = \mu_{ij} \quad \text{AND} \quad var(CA_{ij}) = \mu_{ij} + \mu_{ij}^2/k$$

μ_{ij} is the exponential of n_{ij}:

$$\mu_{ij} = exp(n_{ij})$$

Which is the predicted value from the generalized linear mixed model of the form:

$$n_{ij} = \beta_1 * BottomTemperature_{ij} + \beta_2 * SurfaceChlorA_{ij} + \beta_3 * BottomDO_{ij} + \mathrm{BottomSalinity}_{\mathrm{ij}} + \beta_4 + \theta_{\mathrm{ij}} + \phi_j + \mathrm{w}(\mathrm{s_i})$$

Model 2 is of the same form as model 1 and incorporates the same covariate structure. Both models use the default diffuse priors on all priors and hyperpriors. All parameters and their respective priors used in the models are as follows:

Table 10

Spatial Model Parameter Key

Parameter	Meaning	Distribution	Prior
μ_{ij}	Mean expected crab abundance from the GLMM	N/A, deterministic	$\mu_{ij} = exp(n_{ij})$
k	Dispersion parameter for negative binomial distribution	Diffuse Gamma	Gamma(0.01,0.001)
$\beta_{1,2,34}$	Covariate fixed effect coefficients	Diffuse Normal	N(0,0.001)
θ_{ij}	Seasonal Random Effect	Diffuse Normal	N(0,0.001)
ϕ_j	Year intercept	Diffuse Normal	N(0,0.001)
$w(s_i)$	Spatial effect at location i	Normal (Gaussian Field)	$GMRF(0, \Sigma)$
Σ	Covariance Matrix for the study area	N/A, deterministic	Matérn covariance function + SPDE

All Parameters estimated in the models, with their meanings and estimation methods.

Rather than incorporate spatial structure using arbitrary zonings, which would lack any finer scale resolution, we elected to use the stochastic partial differential equations (SPDE) approach interfaced within R-INLA (Martins et al., 2013). This approach incorporates a spatial random effect (a Gaussian Markovian Random Field GRF) that is indexed in space and can account for the spatial dependency at a finer resolution and with complex structures (Godin et al., 2014). This approach is mathematically complex but allows for a faster estimation of spatial dependency at a finer scale than traditional estimations of GMF's (Lindgren & Rue, 2015). The SPDE approach imposes a mathematical function (the Matérn correlation function) on the structure of the covariance matrix (Σ) to aid in computation time as the covariance matrix can be cumbersomely large (Zuur et al., 2017). The Matérn correlation function has several parameters, which once known, allow the covariance matrix (Σ) to be known. To estimate the parameters of the Matérn correlation function INLA first solves an equation known as the continuous domain stochastic partial differential equation (SPDE). To accomplish this a mesh is created over the study area, with vertices at sampling locations and edges connecting them, creating a triangular mesh known as a Delaunay triangulation. Once this mesh is created the vertices can be assigned weights by solving the SPDE equation, and this network of weighted vertices approximates the full GMRF (Lindgren et al., 2011). The general idea behind Gaussian random fields and geostatistics in general is that things closer in space to one another will be more correlated than measurements taken further apart, this is Tobler's Law (Miller, 2004). The distance between the SEAMAP stations ranged from 0 to 1300 km apart, so geographic distances between sampling stations impact the weight of the spatial correlation.

RESULTS

Condition and Reproductive Output of Spawning Females Collected Offshore

Sample collection for reproductive analyses occurred on each state and federal leg of the SEAMAP shrimp and groundfish survey for both the Summer and Fall sampling periods of 2017. Sampling of Texas and Florida water was completed by NOAA personal and was included with NOAA data deliveries. Females were sampled off the coast of each of the survey's participating states, including the waters near Apalachicola in Florida. This was an area where extensive tagging was conducted in the spring, confirming their presence in Florida's offshore habitats.

Table 11

Reproductive Analysis Sample Collection

Sampling Agency	Number of Stations	Number of Crabs Collected	Number of Ovigerous Females
NMFS	196	93	51
LDWF	23	16	10
MDMR	12	6	4
ADMR	7	3	2

Number of samples collected during each leg of the 2017 summer groundfish survey of SEAMAP.

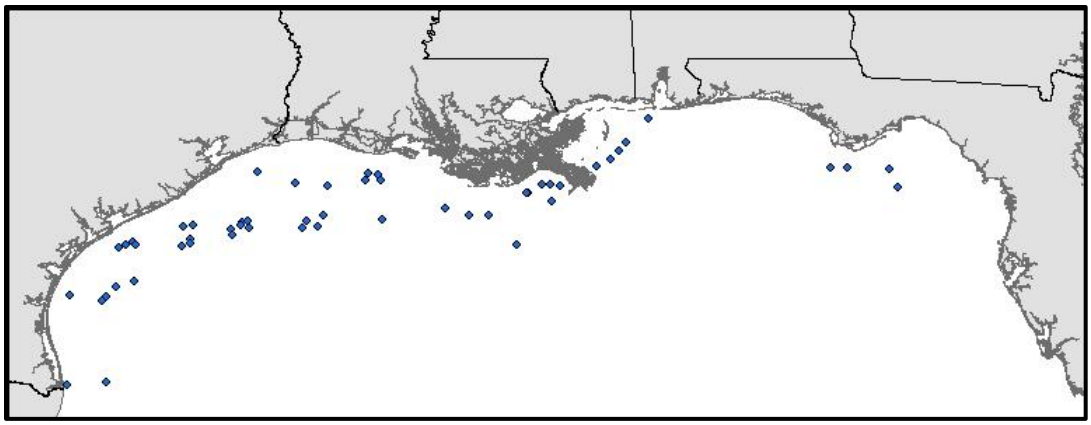

Figure 22. SEAMAP 2017 Specimen Collection Sites

Locations of female crabs collected during the 2017 summer groundfish survey of SEAMAP.

A total of 114 mature female blue crabs were collected during the summer season's survey period, with the majority coming from stations of the coast of Texas and Louisiana. A total of 11 mature females were collected from the fall 2017 season of the SEAMAP survey. Five of the eleven females were egg bearing during the fall sampling season. During summer, the vast majority of crabs collected offshore were spawning capable, while a lower percentage of crabs were spawning capable during the Fall survey (Table 10). Few crabs had mated recently during summer (1.8%), and none had mated recently during fall. The parasitic barnacle *Octolasmis muelleri* was commonly found on the gills of crabs, with 67.5% prevalence in summer and 100% prevalence during fall.

Table 12

Reproductive Analysis Summary

Sampling Season	% Ovigerous	% Spawning Capable	Recently Mated	% w/ Parasitic Barnacles	Mean Egg Diameter
Summer 2017 N = 114	59%	77%	1.8%	67.5%	239.8 ± 17.8 um
Fall 2017 N = 11	36%	36%	0	100%	N/A

Information on the health and spawning state of females collected during the 2017 summer and fall SEAMAP groundfish surveys.

Fecundity ranged from 1.6 to 8.9 million eggs in crabs collected offshore, and was strongly related to carapace width, with larger females having higher fecundity (Figures 23–25). Both candidate models showed similar fits for the data, with the log-link GLM showing a slightly smaller underestimation of fecundity for crabs at the larger size ranges (> 180 mm carapace width). DIC scores confirm that the model 2 outperformed model 1 in predictive performance.

Table 13

Fecundity Model Comparisons

Model	Penalized Deviance	$\Delta\ DIC$	Bayesian P-value
GLM, identity link	185.8	29.9	0.472
GLM, log link	155.9	0	

Deviance information criterion scores for model 1 (identity link GLM) and model 2 (log link GLM). Smaller penalized deviance values correspond to higher predictive performance of the model.

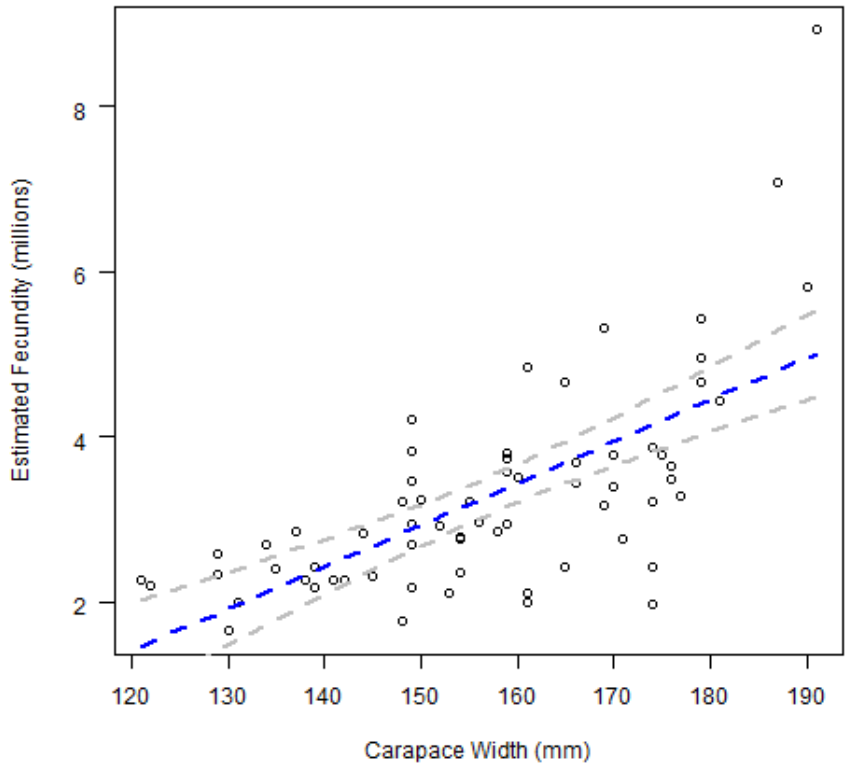

Figure 23. Fecundity and Carapace Width GLM

Estimated fecundity as a function of carapace width for females collected during the 2017 summer groundfish SEAMAP survey. Median estimate (blue) and 95% credibility intervals of bayesian GLM using an identity link are shown.

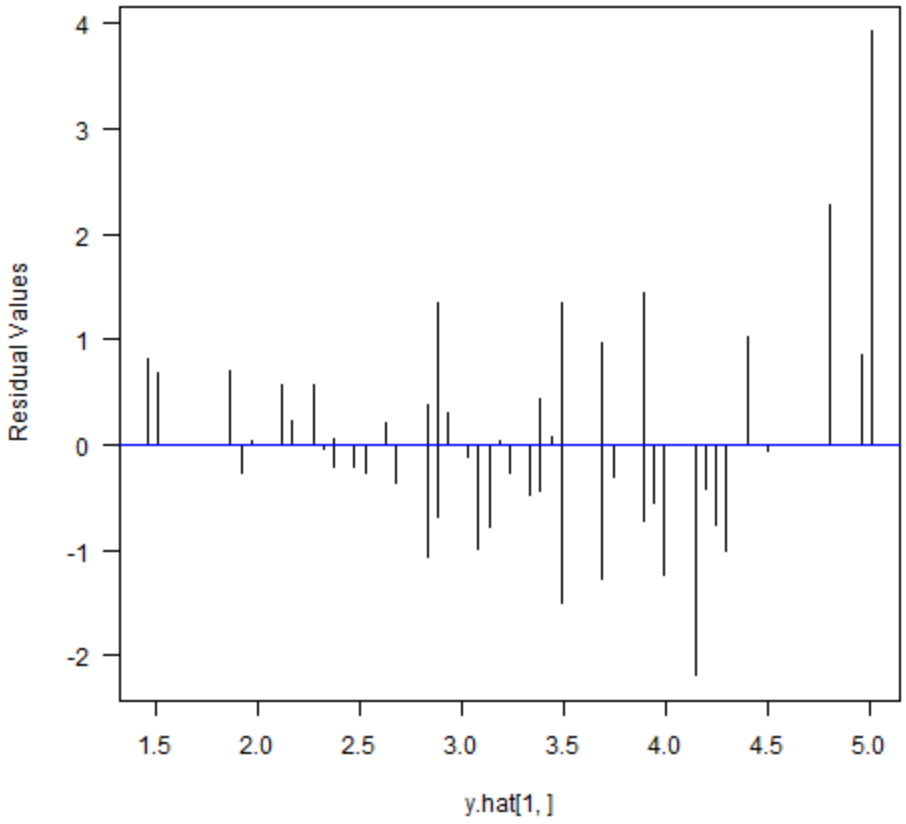

Figure 24. Fecundity and Carapace Width GLM Residual Plot

Residual deviance (gray bars) from median fecundity estimate (blue line) from bayesian glm using the identity link.

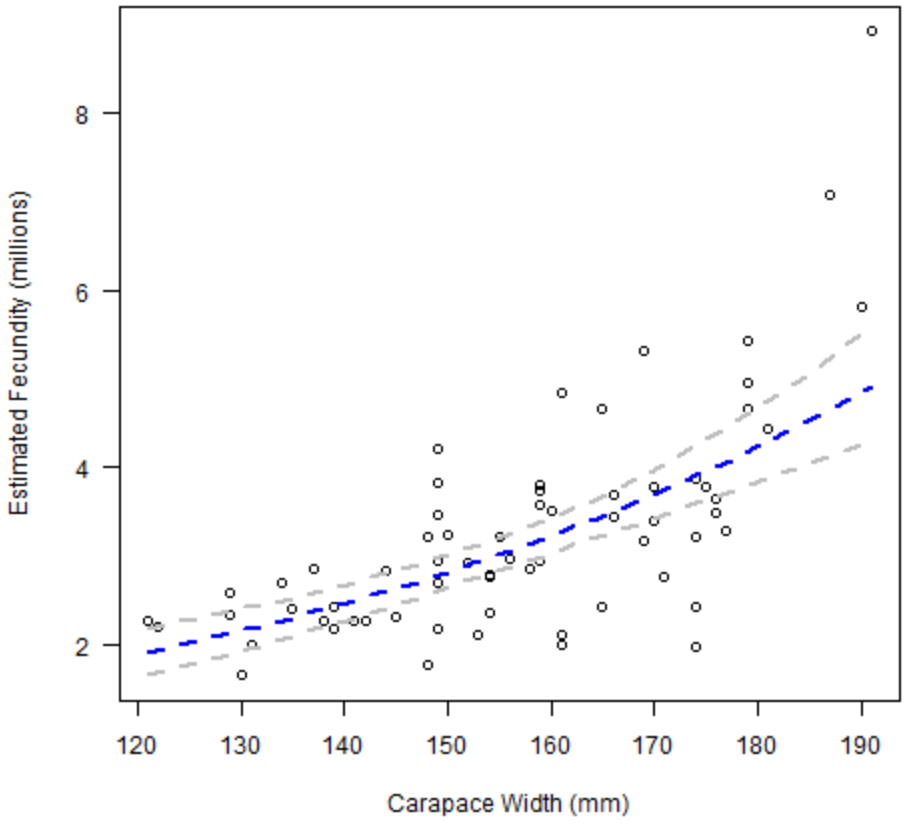

Figure 25. Fecundity and Carapace Width Log Link GLM

Estimated fecundity as a function of carapace width for females collected during the 2017 summer groundfish SEAMAP survey. Median estimate (blue) and 95% credibility intervals of bayesian log GLM are shown.

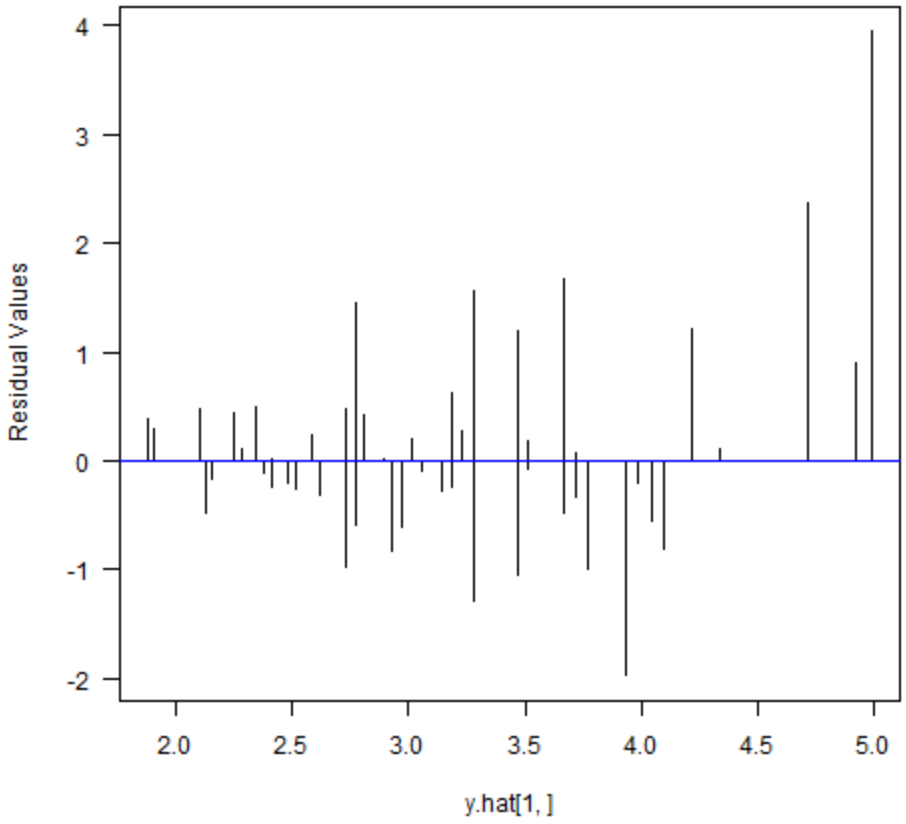

Figure 26. Fecundity and Carapace Width Log Link GLM Residual Plot

Residual deviance (gray bars) from median fecundity estimate (blue line) from bayesian glm using the log link function.

Table 14

Parameter Estimates for Fecundity Models

Model	Intercept	Slope Coefficient
GLM, identity link	-4.68 ± 1.11	0.05 ± .007
GLM, log link	-1.021 ± 0.30	0.014 ± .002

Intercept and slope estimates for model 1 (identity link GLM) and model 2 (log link GLM).

Distribution and Abundance of Female Blue Crabs in Offshore Waters from Historical SEAMAP Data

Although not all blue crabs collected in the SEAMAP surveys are sexed, of the crabs that were sexed during the 15-year study period, 91% were female. A linear regression of the SEAMAP survey data showed a negative relationship between year and mean annual blue crab catch per unit effort over the study period ($p < 0.01$) over the 16-year period. However, mean CPUE estimates are a poor estimate of central tendency for the dataset as it is highly overdispersed, with many zero-catch samples observed (84% of all observations). If we examine recent years' catch in the context 15-year mean CPUE (0.57 crabs per 30min. trawl), this decline is supported, as 9 of the past 16 years fall below the long-term mean.

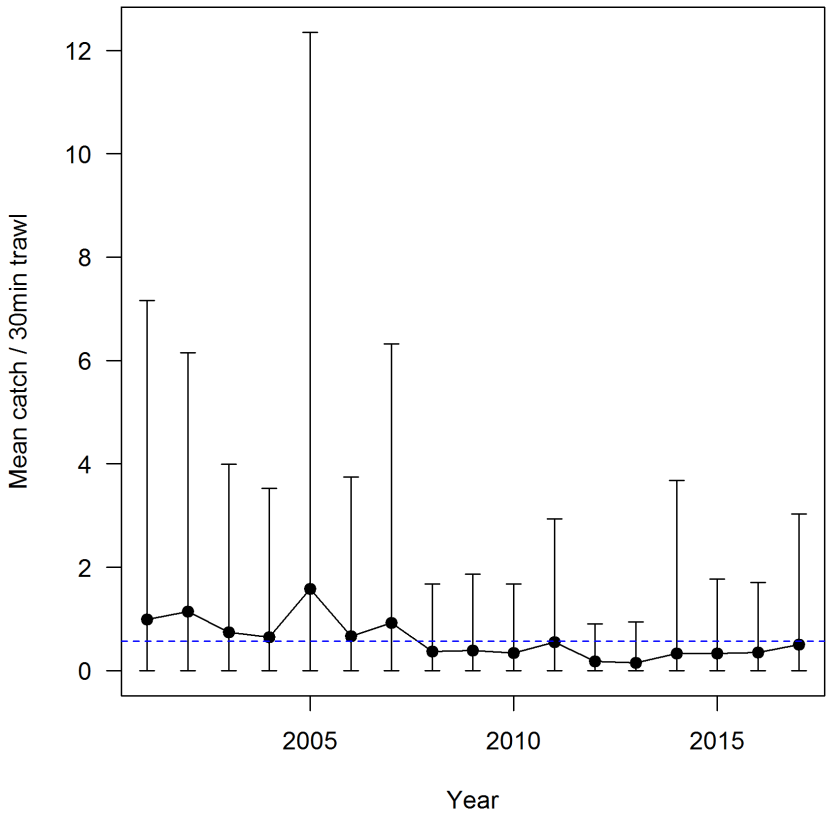

Figure 27. SEAMAP Mean CPUE Timeline

Timeline of mean yearly blue crab catch and associated standard deviation estimates from the SEAMAP historical dataset. Mean crabs/30 min. over the same period is shown in blue.

Blue crab CPUE was also spatially variable across the survey area, with blue crab presence more common along the coasts of Texas and Louisiana and much lower catch numbers along Florida's west coast (Figures 28, 29). Blue crab catch was conspicuously absent from the sampling conducted on Florida's western coast for both seasons. From previous work done, and from our own tagging research blue crab presence in these areas has been established. Further analyses were conducted on a spatial subset of SEAMAP

data from Destin, FL westwards to eliminate any uncertainty that may be tied to sampling difficulties off Florida's coast.

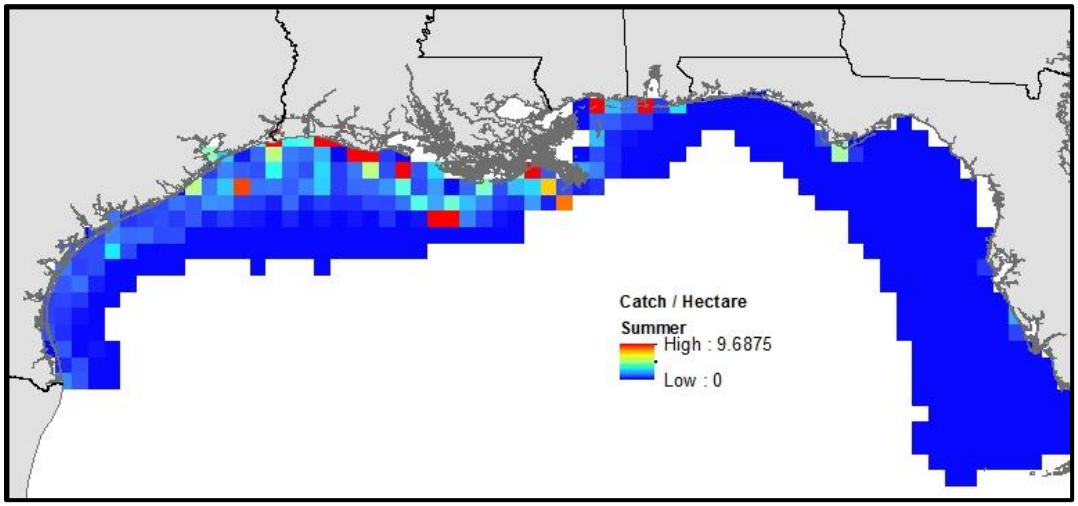

Figure 28. SEAMAP Summer Station Locations 2001-2016

Mean blue crab catch/ hectare from the summer sampling period for the years 2001-2016 aggregated into 0.25° x 0.25° grid cells.

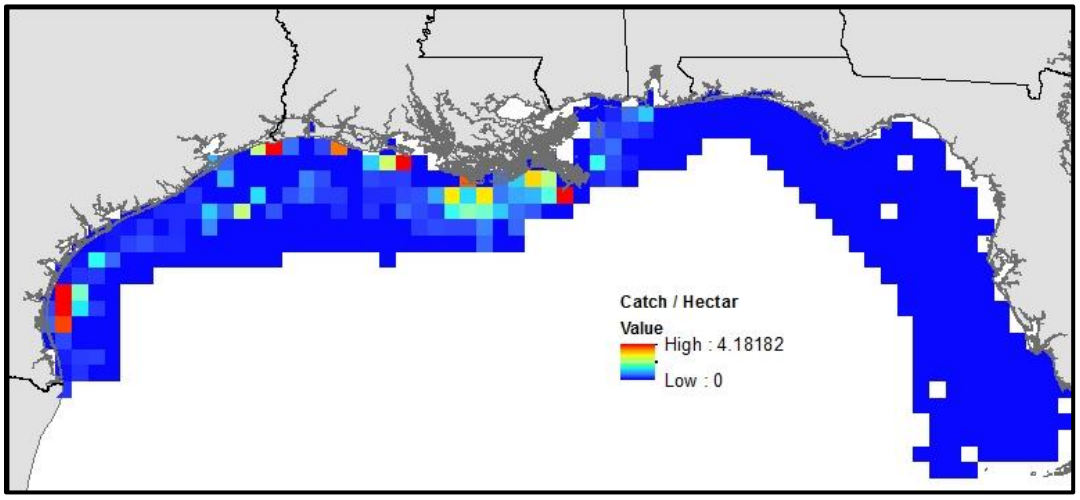

Figure 29. SEAMAP Fall Station Locations 2001-2016

Mean blue crab catch/ hectare from the fall sampling period for the years 2001-2016 aggregated into 0.25° x 0.25° grid cells.

Spatio-Temporal Model

The constrained Delauney triangulation mesh was created with the minimum number of nodes allowed (n = 9602) to aid in computation time, and because the density of the mesh was sufficient for any small scale spatial structures to be detected. The mesh was densest in areas of high sampling and less dense in areas of sparse sampling. A boundary around the sample area is included to minimize edge effects. Spatial correlation structure incorporated using the SPDE method showed lower DIC values than models without explicit spatial correlation structure. Spatial correlation persisted for several hundred kilometers, becoming negligible around 250 kilometers.

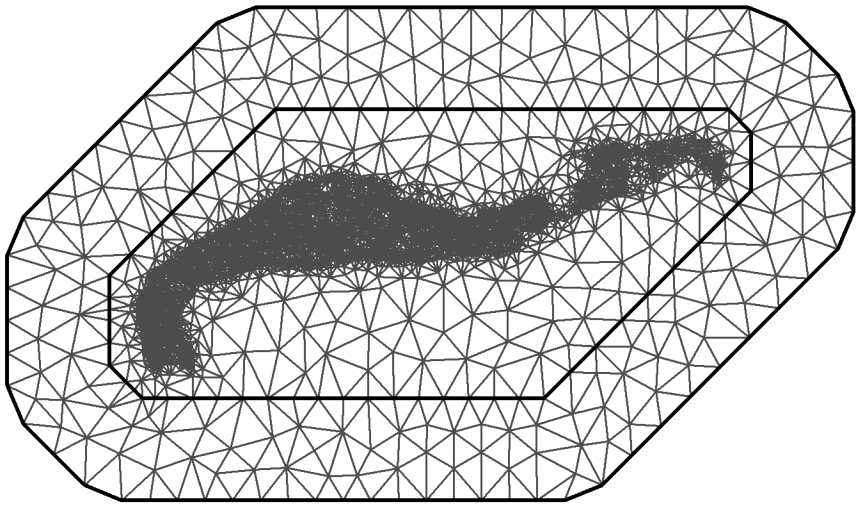

Figure 30. Constrained Delauney Triangulation of Study Area

Constrained Delauney triangulation mesh created for the estimation of the GMRF for the SPDE method for adding spatial correlation structure. Triangles connect nodes which have an indexed weighted value associated with the correlation structure.

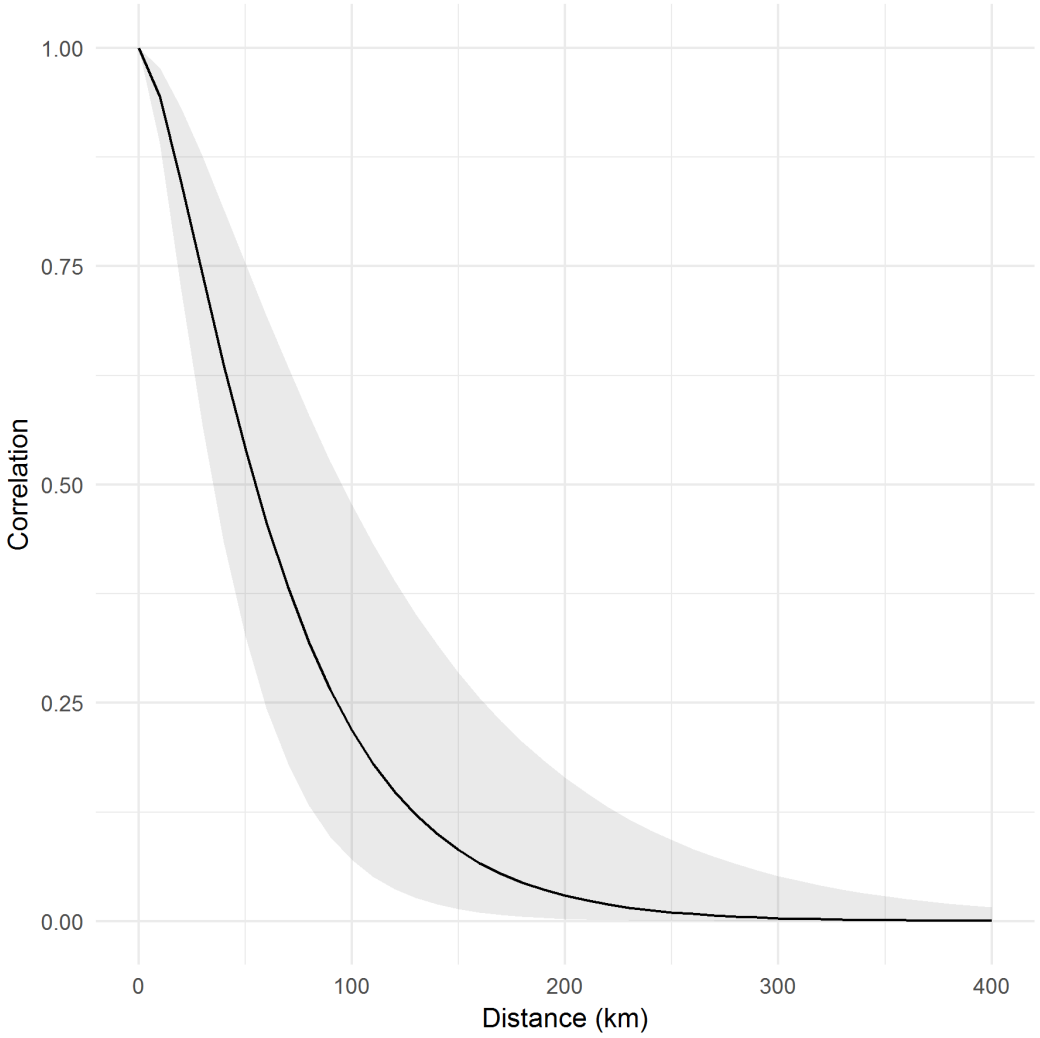

Figure 31. Spatial Correlation Structure from Matérn Function

Decline in spatial correlation with increasing distance between samples estimated from the Matérn correlation function. Range of the spatial correlation (where observations become statistically independent) is around 250km.

Based on DIC comparisons between the negative binomial GLMM without spatial structure, and the same model with spatial structure added using the SPDE method, the model accounting for spatial correlation showed better predictive performance; however, The incorporation of the spatial effect in our model removed the significance of chlorophyll-a, adjusted the dissolved oxygen to a positive correlation. Temperature was positively correlated in both, with salinity non-significant in either.

Table 15

Offshore Model Comparisons

Test Statistic	**NBGLMM**	**Spatial NBGLMM**
Δ DIC	782.155	0
Effective number of parameters	23.40	217.96
Marginal Log-Likelihood	-4560.73	-4256.90

DIC estimates for final model candidates, with and without the spatial correlation term.

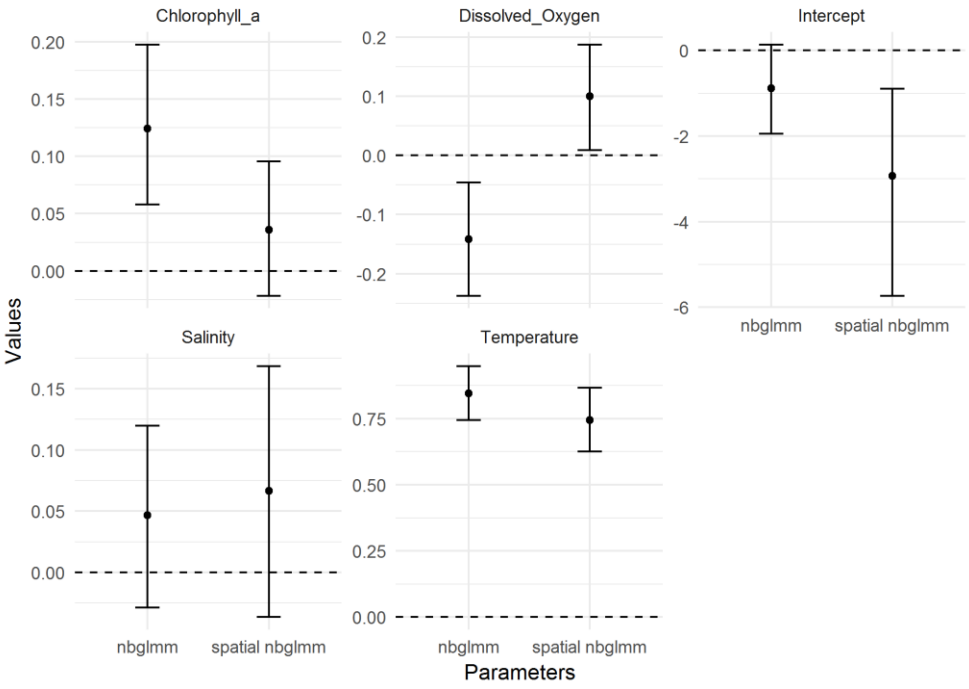

Figure 32. Spatial and Non-Spatial Model Fixed Effect Comparisons

Median marginal posterior estimates (points) and 95% credibility intervals (bars) for the fixed effects of the original negative binomial GLMM model, and the same model with the spatial correlation effect term.

The posterior mean spatial field estimated for the model tracked the sampling densities across the study area and showed higher correlation structure and estimated abundances around land masses like the Louisiana Birdfoot as intended. Spatial correlation was highest in areas of high sample densities and in areas of higher blue crab catch.

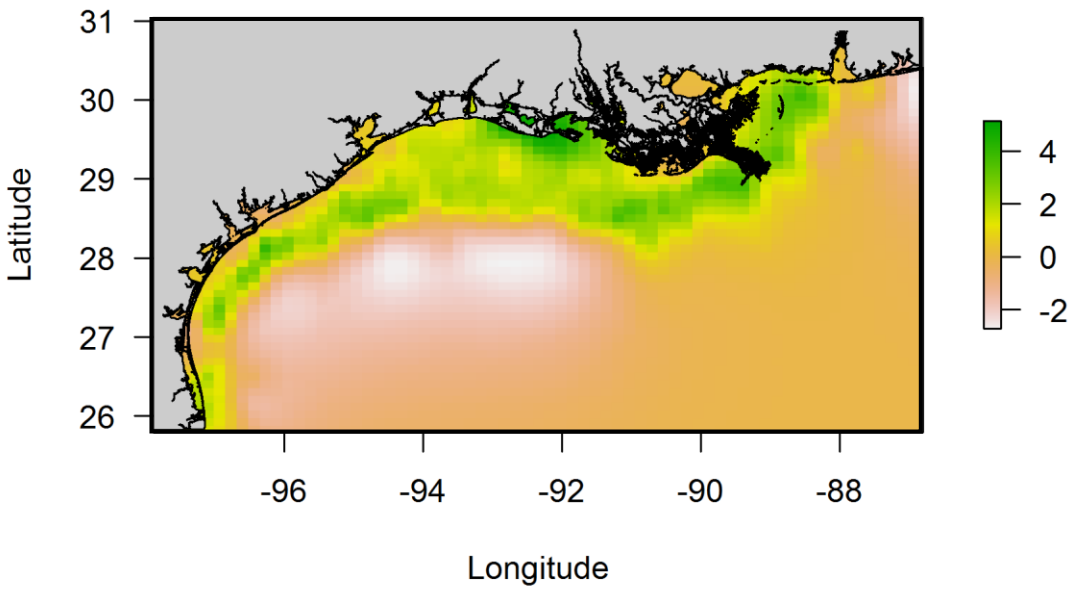

Figure 33. Posterior Mean Random Spatial Field from Spatial NBGLMM

Mean posterior estimate of the GMRF, higher values (green) are associated with stronger spatial correlation structure and upwards of 4x predicted crab abundances. Orange and white values correspond to a diminished spatial correlation and lack of association to predicted abundance.

Table 16

Spatial Model Fixed Effects Summary

Fixed Effects:	**Mean**	**Sd**	**2.5% Quantile**	**Median**	**97.5% Quantile**	**Significance**
Intercept	-2.93	1.20	-5.73	-2.7896	-0.90	-*
Salinity	0.0664	0.05	-0.04	0.07	0.17	
Temperature	0.74	0.06	0.62	0.74	0.87	+*
DO	0.10	0.05	0.01	0.10	0.19	+*
Chlorophyll A	0.04	0.03	-0.02	0.04	0.10	

Summary Statistics of the final INLA negative binomial GLMM model

Table 17

Spatial Model Random Effects Summary

Model hyperparameters:	Mean	sd	2.5% Quantile	Median	97.5% Quantile	Significance
Size (k) for NB observations	0.39	0.02	0.34	0.39	0.43	+*
Precision for Year	3.30	1.74	1.53	3.13	6.09	+*
Precision for Season	2.09	1.88	0.25	1.56	7.08	+*
Theta1 for w	1.88	0.13	1.61	1.88	2.13	+*
Theta2 for w	-4.05	.41	-4.78	-4.08	-3.17	+*

Summary Statistics of all posterior estimates for hyperparameters in the model.

DIC values for the model containing the spatial term were lowest of all test models, despite the increase in effective number of parameters. Once spatial correlation was integrated into the model, changes in the dominant bottom cover type no longer captured variation of blue crab abundance. However, all random effects remained significant predictors in the model. The dispersion parameter k, or the size parameter for the negative binomial distribution, was positively significant indicating that abundance was clustered. The fall sampling season corresponded to lower predicted abundance compared to the summer season for all models, and yearly random effect impacts varied widely among the years included, with a general decline over the study period.

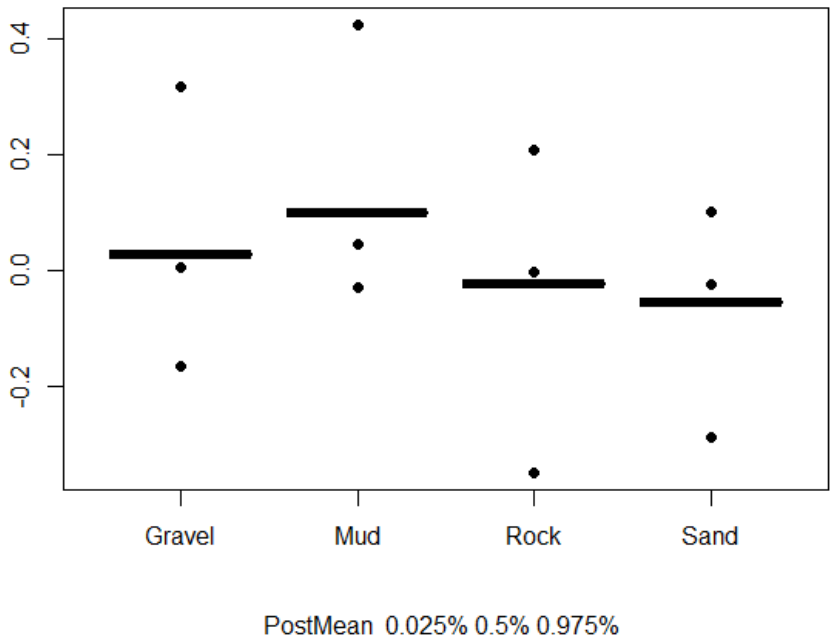

Figure 34. Dominant Bottom Cover Random Effect for NBGLMM

Mean marginal posterior estimates (horizontal bars) and the 2.5%, 50%, and 97.5% posterior estimates (points) for the random effect of dominant bottom cover type for the final model candidate without the spatial term.

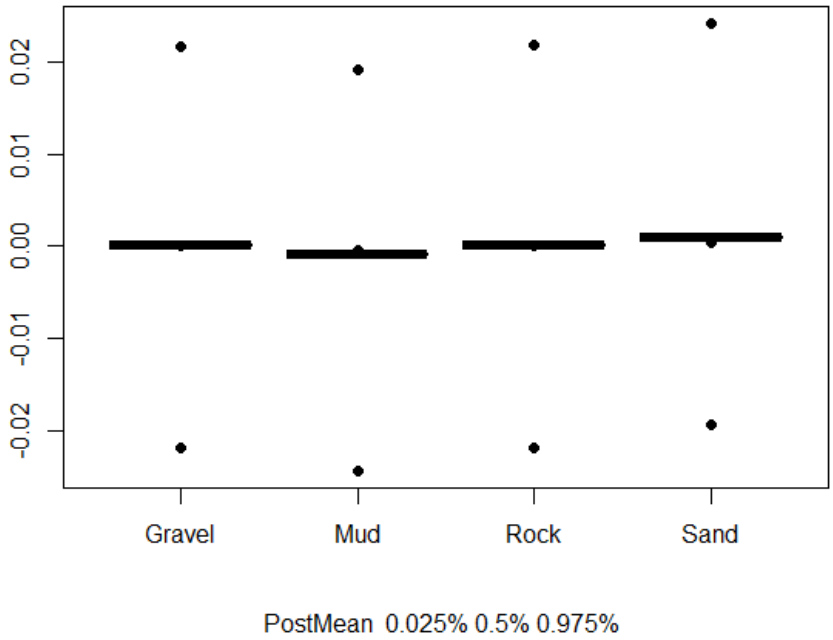

Figure 35. Dominant Bottom Cover Random Effect for Spatial NBGLMM

Mean marginal posterior estimates (horizontal bars) and the 2.5%, 50%, and 97.5% posterior estimates (points) for the random effect of dominant bottom cover type for the final model candidate that incorporated the spatial term.

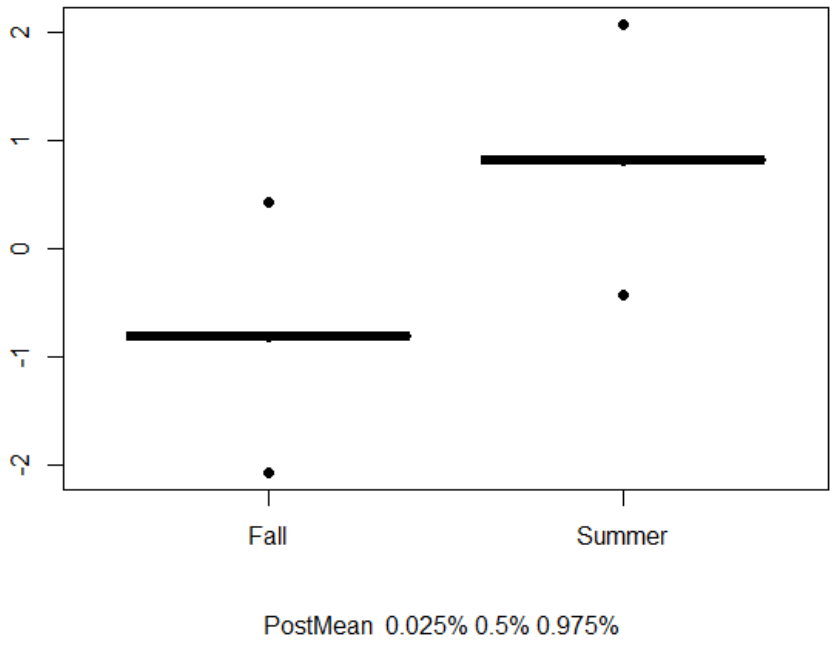

Figure 36. Seasonal Random Effect for Spatial NBGLMM

Mean marginal posterior estimates (horizontal bars) and the 2.5%, 50%, and 97.5% posterior estimates (points) for the random effect of sample season for the final model candidate that incorporated the spatial term.

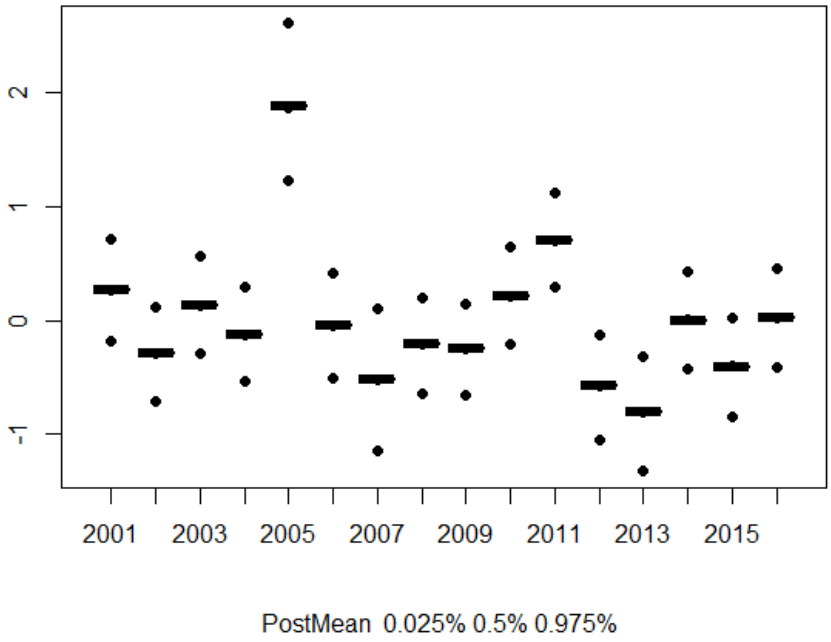

Figure 37. Year Random Effect for Spatial NBGLMM

Mean marginal posterior estimates (horizontal bars) and the 2.5%, 50%, and 97.5% posterior estimates (points) for the random effect of sample year for the final model candidate that incorporated the spatial term.

Patterns in the fitted values plotted against the residual values of the model show that there remains uncertainty in the model and that predictive performance may still be low, with decreasing accuracy with increasing values.

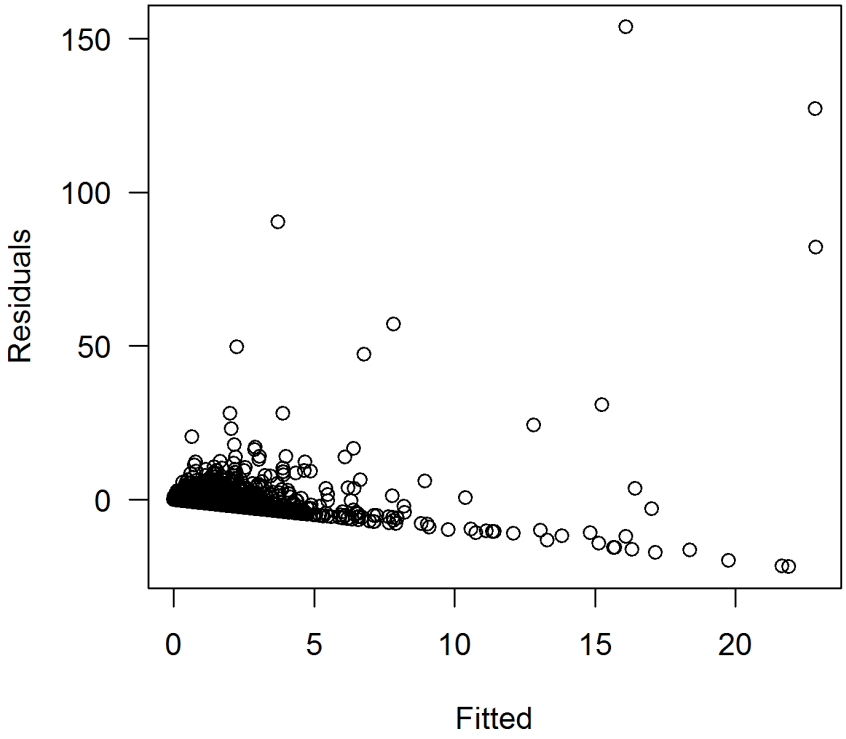

Figure 38. Fitted and Residual Plot for Spatial NBGLMM

Comparison of values fit from the spatial model candidate and their corresponding Pearson residuals.

DISCUSSION

We examined the occurrence and reproductive output of female blue crabs in offshore waters, using samples and data from the fishery-independent SEAMAP groundfish (trawl survey). Mature female blue crabs are commonly caught in this survey as far as 150 km from the coast and are frequently caught while ovigerous or showing evidence of potential future reproductive output (as evidenced by visible mature ovaries). Fecundity was high for females collected offshore, and comparable to previously published fecundity estimates from inshore-spawning crabs. Graham et al. (2012) estimated fecundity of crabs spawning in Mississippi Sound to range from 1–7 million eggs (Graham et al., 2012). Fecundity estimates observed here (mean = 3.28 ± 1.25 million eggs) were similar, suggesting that these offshore spawning crabs are producing broods of similar egg count to females spawning inshore. Furthermore, the eggs carried by the offshore females examined here were of similar diameter (239.8 ± 17.9 μm) to those measured by Graham et al. (2012) for females spawning in Mississippi Sound during the summer/fall (238.6 ± 13.0). Combined, these results indicate that females spawning offshore are likely making as substantial a reproductive contribution on a per-capita basis as females spawning inshore.

Although females spawning offshore are producing high numbers of apparently viable eggs, densities offshore are quite low, as would be expected given the dilution effect as that occurs as females migrate out of their home estuaries. Additionally, densities of spawning females in offshore waters have declined in recent years, reflecting declines observed in several Gulf states (Anderson et al., 2017, LDWF, 2016). The density from the 15-year SEAMAP dataset analyzed here was 0.29 ± 2.04 crabs hectare^{-1},

while inshore densities inshore are likely much higher. Yet these offshore females are spread over a large area, and thus their total abundance is likely quite high. Similarly, in Georgia, Ogburn and Habegger (2015) found abundance in offshore areas (but considering only the 2–10 m depth range) of 1.58 crabs hectare^{-1} in 1991, with a decline over time. The authors also posit that despite a less dense population offshore, the total abundance of the offshore population is comparable to the denser inshore population.

A second goal of this study was to develop a spatially explicit predictive model to examine the distribution and occurrence of female blue crabs in the Gulf of Mexico. The decision to incorporate spatial structure into the catch model was a technical reach, but it was a decision reached after extensive attempts at less complex models. The SEAMAP catch data were highly zero-inflated, necessitating the use of a model that could accommodate the high degree of overdispersion in the data. Several candidate models were run in JAGS using a zero-altered Poisson distribution. These models explicitly separated the data into a binary model that looked at the relationship between the covariates and absence or presence of blue crabs, and an abundance model that would then address the difference in count data, using the same set of or potentially different covariates. The weaknesses of these approaches were, that they were computationally intensive, taking several hours to converge, and that they weren't able to estimate any of the large abundance events that were observed. They also did not incorporate spatial correlation in the observations. The easiest method to incorporate spatial structure into these models is with a group level random-intercept effect that would correspond to some arbitrary geographic boundaries that we designated. Since one of the main objectives of the study was to identify areas of higher offshore abundance we elected to use the SPDE

approach as an alternative. The advantages of incorporating spatial correlation structure in this way is twofold. Spatial correlation is incorporated at the scale of the study design and indexed spatially, rather than at some arbitrary zoning level. This allows for the identification of clustering in the data, so in the event that an underlying geographic feature or proximity to a coastal area played a large role in predicting our response variable these patterns would be detected on the scale that they occurred. Another advantage of performing the analyses through R-INLA was the ability to run model comparisons in a matter of minutes, rather than hours as computation using INLA is roughly 300x faster than posterior sampling using MCMC methods. INLA also offered similar model specification flexibility with regards to the specification of priors and variance structures.

The incorporation of the spatial effect in our model removed the significance of temperature and dissolved oxygen and chlorophyll-a from our model. One reason this may have occurred is that dissolved oxygen and chlorophyll-a concentrations are themselves spatially correlated, as they are driven by (or the direct sign of) regional biological activity. Although our model was not able to accurately predict observed abundance estimates from the trawl survey, and there were patterns in the residual plots, they were lesser than all other model candidates, and DIC values confirmed greater model performance. The model may not be performing as well as desired may be due to a number of reasons. First, we may be missing an important covariate in the model, like prey availability, which is not quantified in the SEAMAP surveys. Second, the SEAMAP survey is conducted in two main trawl sampling seasons over a large geographic area. Any small scale temporal patterns are likely to have poor representation with this

sampling design. Catch data from the survey has been used successfully to predict the abundances of various functional groups in the Gulf of Mexico using spatially explicit Generalized-Additive Models (Drexler & Ainsworth, 2013), however without good predictive covariates this method would likely show similar results to our analyses.

One important question to consider when considering the potential contribution of the offshore portion of the Gulf of Mexico blue crab spawning stock is the fate of larvae spawned great distances offshore. The successful spawning of multiple offshore clutches does not guarantee that the larvae are successfully recruiting back to the inshore nursery habitats used by juveniles. There may be some distance from shore above which larvae are essentially "lost", never making it back into estuaries. This should be considered when evaluating the reproductive contribution of the offshore spawning stock and could be resolved through a larval transport modeling approach.

Another equally important question, is why do are blue crabs almost completely absent from the SEAMAP data collected on the West Florida Shelf? In the spring of 2017 we were able to tag over 800 female blue crabs in waters off the coast of Steinhatchee, FL. Many of these females, which were already in the coastal Gulf of Mexico at the time, continued migrating North crossing over 100 km of offshore habitat that is sampled by the SEAMAP survey every year. Yet during the summer and fall SEAMAP surveys conducted in 2017 by Florida Fish and Wildlife Conservation Commission, not a single blue crab was caught (S. Stahl and R. Jones (FWC), personal communication). Females are known to occupy these habitats, and there is intense fishing pressure along the coast for this reason. To have such consistent zero-catches for blue crabs for the region is concerning, and part of the reason why our analyses were restricted

to a Western subset of the data. One possible explanation is that the migratory period for females along the West coast of Florida has already taken place by the time SEAMAP begins sampling each year. Anderson et al. (2017) noted the peak spawning season for the Texas blue crab population now begins sooner than it had in the past, shifting from peak abundance in the late summer and early fall to a spring spawning peak in March–April. Florida is at a similar latitude to Texas, so it is possible that this is the case, but without any tagging data outside of the spring season, and no SEAMAP data we were not able to assess this hypothesis.

Offshore numbers of female crabs are difficult to estimate because they aren't directly sampled for with any real frequency, and their population density decreases with increasing distance from land. There is the potential for offshore spawning populations to contribute greatly to the inshore populations by sheer amount of habitable space in the Gulf of Mexico. However; by all estimates the offshore spawning stock has been declining over the past few decades. Mean estimates obtained from SEAMAP surveys are a poor stand-alone estimate of abundance as the data is zero-inflated and mean catch is a poor measure of central tendency. Clearly, further work is necessary to determine the relative contribution of offshore-spawning females to the Gulf of Mexico blue crab spawning stock.

CHAPTER IV – SUMMARY AND CONCLUSIONS

Blue crabs are economically, ecologically, and culturally important in the Gulf of Mexico. They support regional fishery worth hundreds of millions of dollars each year (NMFS 2016), and they play a critical role in estuarine food webs (Hines et al., 1990; Scharf and Schlicht, 2000; Virnstein, 1977). Their populations have seen declines in many areas, with their management strategies and stock delineations being rightfully called into question (GSMFC 2013). Mature female crabs travel large distances as part of their seasonal spawning migrations, and can travel hundreds of kilometers, with estimated mean travel rates of several kilometers per day. Females also regularly traveled outside of their home management jurisdiction (Aguilar, 2005; Chapter 2 of this thesis). Based on mark-recapture results, it is clear that mature females in the North-Central Gulf of Mexico, between Lake Pontchartrain and St. Andrews Bay regularly mix, both within coastal areas and offshore. Combined with the potential for long-distance dispersal during the 30–50 day planktonic larval phase, this evidence provides further support for assessment and management at a geographic scale larger than the current state management jurisdictions.

The Gulf States Marine Fisheries Commission recently proposed a two-stock structure for blue crabs in the Gulf of Mexico, with the break around Cape San Blas, FL (GSMFC 2013). Results support this structure, as migratory patterns on the West coast of peninsular Florida were consistent with previous work that showed northwestward movement but few crabs crossing Cape San Blas (Steele, 1991). Movement patterns in other areas (which fall within the western stock, based on the GSMFC definition) to be

less uniform once crabs exited their home estuary, supporting a high level of mixing in these areas.

The spawning migration does not end at estuary mouths or even in the coastal ocean; mature female blue crabs continue migrating throughout their life (Darnell et. al. 2012; Hench et al., 2004). Especially in the northern Gulf of Mexico, where estuarine salinities are often quite low, spawning females migrate substantial distances offshore, being caught in the fishery-independent SEAMAP trawl surveys as far as 150 km from shore. These crabs are actively spawning multiple clutches of eggs once offshore, and these clutches appear viable. This offshore spawning stock is not typically considered in current stock assessments or management plans, which likely limits the accuracy of present stock assessments and effectiveness of present management plans.

Taken as a whole, the results of this thesis support a high level of mixing among the estuaries in the Gulf of Mexico, and suggest that the effectiveness of assessment and management efforts could be improved by increasing the geographic scale of these efforts. Future work linking spawning locations identified here with regional current patterns and larval behavior through larval transport modeling (i.e., Bierman et al. 2016, North et al. 2008), could provide additional insight on how female migratory patterns and spawning locations influence recruitment patterns and connectivity among estuaries and further inform decisions related to the relevant spatial scale for management and assessment.

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